EVOLUTIONARY BIOLOGY OF ANADROMOUS, RESIDENT, AND LANDLOCKED ARCTIC CHARR (*SALVELINUS ALPINUS)* IN LABRADOR, CANADA

by

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For Mom and Dad

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ABSTRACT

The breadth of biological forms observed in nature is found in miniature within Arctic Charr (*Salvelinus alpinus*). This species' incredible phenotypic variation and distinct morphs makes it highly useful for investigating the genetic sources of morphological differentiation and reproductive isolation. In this thesis I used microsatellite, mtDNA, and SNP data to assess the neutral and adaptive genetic characteristics of Arctic Charr morphs within Labrador, Canada (a region only recently deglaciated ~9000 years ago and subsequently colonized by charr). In addition to populations of anadromous and landlocked morphs, this work found evidence for small resident charr that occur in sympatry with, but are genetically distinguishable from, anadromous charr. Multiple landlocked lakes were also found to harbour genetically distinguishable, size-differentiated, sympatric morphs. Investigation of the charr colonization history of this region using mtDNA revealed the secondary contact and introgression of three charr glacial lineages (Arctic, Atlantic, and Acadian). However, mtDNA did not consistently differ by morph type and the sympatric morphs detected in this region likely evolved following the introgression of these three glacial lineages. While there was generally little evidence of genetic parallelism, a few key SNPs, genes, paralogs, and genomic regions consistently differed between sympatric size-differentiated morphs and between allopatric landlocked and anadromous morphs. Furthermore, some of the loci that differentiated sympatric resident and anadromous morphs also differentiated allopatric landlocked and anadromous populations, suggesting that the loss of anadromy may be genetically predictable. However, a population's genetic characteristics were not solely a function of morph type but were uniquely dictated by the interactive effects of morph life history, geography, glacial history, and environment. A review of the genetic differences between sympatric morphs in Salmonidae confirmed the interactive influence of glacial history as well as contemporary neutral and adaptive processes on incipient speciation within salmonids. This work reveals that salmonids, and particularly Arctic Charr, are excellent models to uncover speciation mechanisms that are potentially relevant across the tree of life. This work therefore has applications for the conservation of morph diversity and implications for our mechanistic understanding of evolution.

LIST OF ABBREVIATIONS USED

ACD – Acadian lineage mitochondrial deoxyribose nucleic acid haplotype

A_R – allelic richness

ARC – Arctic lineage mitochondrial deoxyribose nucleic acid haplotype

ATL – Atlantic lineage mitochondrial deoxyribose nucleic acid haplotype

bp – base pair

BP – before present

CI – confidence interval

DNA – deoxyribonucleic acid

FDR – false discover rate

FL – fork length

GEP – Google Earth Pro

GO – gene ontology

H_E – expected heterozygosity

HKY85+I+G - Hasegawa-Kishino-Yano 1985 Model + invariable sites + gamma model

H_O – observed heterozygosity

HSD – honest significant difference

HWE – Hardy Weinberg equilibrium

IBD – isolation by distance

K – number of clusters

k - 1000

LGM – last glacial maximum

LP -location priors

MAF – minor allele frequency

MCMC – Markov chain Monte Carlo

MHC – major histocompatibility complex

mtDNA – mitochondrial deoxyribonucleic acid

mya – million years ago

nDNA – nuclear deoxyribonucleic acid

$\widehat{N}_e$ – effective population size estimate

PCoA - principal coordinates analysis

PCA – principal components analysis

PCR – polymerase chain reaction

P_{crit} – minimum allele frequency

QC – quality control

QTL – quantitative trait locus

RDA – redundancy analysis

RNA – ribose nucleic acid

SNP – single nucleotide polymorphism

WGD – whole genome duplication

ACKNOWLEDGEMENTS

I think a PhD can sometimes be idealized as a solitary quest into the unknown, slaying dragons in search of some capital "T", truth. But my "dragons" were mostly bugs, both entomological and virtual. And though this thesis work required a great deal of solitude, from dreamlike nights spent staring up at the northern lights in the wilds of Labrador to long days spent huddled over the dim glow of a computer screen, I was never alone. Whatever value you glean from this work is owed to all the people who helped me through the wilderness.

First, thanks to my supervisor, Dr. Daniel Ruzzante, who welcomed me into his lab almost 8 years ago and somehow still hasn't changed the locks on me. Thank you for always having my back; I am grateful for your continued support, guidance, and insight. I would also like to particularly thank Dr. Ian Bradbury who kindly gave me the opportunity to return to Labrador for additional charr sampling. Thanks for your advice and assistance in our "charr meetings" which were essential to the completion of this thesis. Along with Dr. Bradbury, thanks go to Dr. Paul Bentzen and Dr. Anne Dalziel for serving on my PhD committee and for challenging me to think more deeply and clearly about this work. Dr. Louis Bernatchez graciously agreed to serve as an external examiner for my defense and provided many insightful comments which greatly improved this thesis. Dr. Christophe Herbinger and Dr. Mark Johnston were not on my committee for this degree yet somehow kept getting roped into my various exam committees. I greatly appreciate impromptu discussions with them on my work in the halls of the LSC.

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“There, but for a twist of DNA, go you or I”

- Joan Slonczewski, *Brain Plague*

“καὶ περὶ μὲν τοὺς ἰχθύας οὕτω ἔχει”

- Herodotus, *The Histories* (2.94.1)

“Oh, what is my theory? This is it. My theory that belongs to me is as follows. This is how it goes. The next thing I'm going to say is my theory. Ready?”

- Monty Python, *Monty Python’s Flying Circus*

CHAPTER 1 - INTRODUCTION

What drives the diversity of forms found in nature is a fundamental question of biology. However, subsequent evolutionary processes can sweep away the genomic signatures of early diversification (Bush 1994; Coyne and Orr 2004; Elmer and Meyer 2011). Recent radiation events in species such as cichlids (Wagner et al. 2013; McGee et al. 2016), Darwin's finches (Zhang et al. 2014; Lamichhaney et al. 2015), and *Heliconius* butterflies (Martin et al. 2013; Kozak et al. 2015) have therefore been instrumental in uncovering the genomic underpinnings of reproductive isolation and adaptive phenotypic differentiation.

However, many questions about the genomic mechanisms of speciation remain unresolved. The temporal and spatial scales over which genetic differences accumulate among incipient species continues to be an active area of research (Matute and Cooper 2021). While recent microallopatry may play a key role in the formation of phenotypically and genetically differentiated morphs, a growing body of literature supports the existence of sympatric speciation (Bush 1994; Johannesson 2001; Via 2001). Historical allopatry followed by secondary contact may also influence contemporary morph differentiation as it could lead to the reinforcement of distinct species (Dobzhansky 1937; Servedio 2004). Alternatively, complete introgression between allopatrically diverged lineages could increase genetic diversity and fuel contemporary radiations (e.g., Feder et al. 2003; Meier et al. 2017; Lamichhaney et al. 2018). In between these two extremes, introgression among hybridizing lineages may be constrained by both selection and evolutionary history resulting in locally nuanced effects on contemporary morph differentiation (Gompert et al. 2017, Mandeville et al. 2019, Marques et al. 2019). Given that many species were separated into distinct refugia during the Pleistocene the descendants of which have recently come into secondary contact (Hewitt 1996, 2000; Bernatchez and Wilson 1998), glacial history may play an important role in shaping speciation. The predictability of speciation, famously characterized by Gould's (1990) thought experiment of replaying the "tape" of life, also remains largely unknown (Blount et al. 2018). Although Gould (1990) advocated for the importance of contingency, increasing evidence suggests parallelism in evolution is possible (Elmer and

Meyer 2011; Blount et al. 2018). However, it is unclear to what extent genetic parallelism will underlie morphological parallelism, nor at what "level" this genetic parallelism is likely to occur (Conte et al. 2012). For example, replicated morphologies could be due to the employment of consistent allelic variation, different mutations in the same gene, or different genetic changes resulting in consistent gene expression (Elmer and Meyer 2011; Jacobs et al. 2020). Genetic comparisons of recent incipient speciation events which are evolutionarily independent (experience minimal contemporary gene flow) (Schluter 1996b) yet share a similar evolutionary history (to ensure a similar genetic starting point prior to speciation) (Elmer and Meyer 2011) are needed to answer these questions.

Given its incredible phenotypic variation (Klemetsen 2013), Arctic Charr therefore offers an excellent natural model to study the factors driving morph differentiation and incipient speciation. Variations in morphology, life history, behaviour, and habitat use have been observed across their Holarctic distribution (Parker and Johnson 1991; Griffiths 1994; Jonsson and Jonsson 2001; Klemetsen 2010). This led to the historical description of up to 11 species of Arctic Charr, though these are now generally considered to be part of a single species "complex" (McPhail 1961; Scott and Crossman 1973). Significant phenotypic differentiation can also be observed between sympatric morphs (Klemetsen 2010). The question of whether this sympatric differentiation has a genetic or plastic basis has been dubbed "the charr problem" (Nordeng 1983). While this species' polymorphism has intrigued researchers for over 100 years (Robinson and Parsons 2002) its cause remains largely undetermined (Klemetsen 2010).

Ancestrally, Arctic Charr were anadromous, that is, spawning in freshwater but undertaking annual marine migrations (Scott and Crossman 1973). It is this morph that likely recolonized the current post-glacial Holarctic distribution of this species (Power 2002a) following the last glacial maximum ~ 20000 years BP (Brunner et al. 2001). Assisted by melting glacial water, anadromous Arctic Charr were often one of the first species to colonize recently deglaciated habitat (Wilson et al. 1996; Power 2002a). A lack of interspecific competition and their inherent capacity for plasticity likely facilitated their subsequent niche expansion, resulting in a radiation of morphologies and life histories (Skúlason et al. 1999). With time and niche stability (Parker et al. 2001), genetic

assimilation (Waddington 1953) is expected. That is, plastic differences between Arctic Charr morphs are predicted to be lost in favour of adaptive genetic differences (Skúlason et al. 1999).

Such polymorphisms are often present within landlocked lakes, where formerly anadromous charr became trapped in fresh water (where they reside year-round) (Klemetsen 2010). Such landlocking could be due to isostatic rebound associated with glacial retreat (Johnson 1980) or due to the loss of anadromy in charr populations due to selection for residency (Finstad and Hein 2012). Cut off from other populations, landlocked lakes have been likened to "inverse islands" (Lassen 1975), and, similar to islands, frequently demonstrate morph radiations (Robinson and Wilson 1994; Robinson and Parsons 2002; Seehausen 2004). In Arctic Charr, a variety of ecologically, morphologically, and genetically differentiated morphs have been found in sympatry in landlocked lakes (Klemetsen 2010). These morphs are typically differentiated by diet and examples include benthivores, planktivores, and piscivores (Jacobs et al. 2020). Such morphs may also differ in spawning time (Westgaard et al. 2004; Corrigan et al. 2011; Garduno-Paz et al. 2012), size (e.g., Gomez-Uchida et al. 2008), isotope signatures (e.g., Power et al. 2009; Woods et al. 2013), parasite content (e.g., Conejeros et al. 2014; Knudsen et al. 2014), prey species composition (e.g., Knudsen et al. 2006; Woods et al. 2013) and morphological characteristics (such as size, fin shape, head shape, body shape; e.g., Arbour et al. 2011; Garduno-Paz et al. 2012). Landlocked sympatric morphs have been well-studied, particularly in European populations, likely due to their occurrence at more southerly latitudes than other Arctic Charr morph types (Klemetsen 2010).

However, the ancestral anadromous morph is still observed across the Arctic (Klemetsen 2010). Unlike many other anadromous salmonids, anadromous Arctic Charr have a short marine period, descending from freshwater habitats with the break-up of ice in spring and returning in fall to spawn and overwinter (Scott and Crossman 1973). It is thought that Arctic Charr cannot adequately osmoregulate in salt water during winter and therefore must return to fresh water to overwinter each year (Finstad et al. 1989). While anadromous charr exhibit natal homing, straying is common (Bernatchez et al. 1998; Moore et al. 2013). Alternatively, charr may spawn in natal habitat but overwinter in non-natal habitat (Moore et al. 2017). Eggs hatch in spring and juveniles will remain in fresh

water for several years before undergoing smoltification after which they undertake annual anadromous migrations (Scott and Crossman 1973). Juveniles may make several anadromous migrations before maturing (Johnson 1980; Jonsson and Jonsson 1993; Rikardsen et al. 2000, 2004) and mature adults may not spawn every year (Scott and Crossman 1973). Anadromous charr have a much longer period of growth and development compared to other anadromous salmonids, though this can vary throughout the species range with faster growth generally found at lower latitudes (Scott and Crossman 1973; Tallman et al. 1996).

In some populations, a resident morph which remains in fresh water year-round co-occurs with the anadromous morph (Johnson 1976; Loewen et al. 2010). Sympatric resident and anadromous morphs differ in morphology (e.g., differences in body and fin lengths, eye diameter; Loewen et al. 2009; Loewen et al. 2010), life history (e.g., differences in migration, maturation time, growth rate; Nordeng 1983; Rikardsen et al. 2004), parasite exposure (Bouillon and Dempson 1989), and prey species consumption (Rikardsen et al. 2000). Anadromous charr typically achieve greater lengths than residents potentially because of better food quality or more favourable temperatures encountered in the marine environment (Rikardsen et al. 2000; Loewen et al. 2010). Size differences might also be due to a developmental trade-off such that anadromous morphs delay maturation in favour of growth whereas residents mature earlier at the expense of growth (Rikardsen et al. 2004). However, large residents are also known to occur in sympatry with anadromous morphs (Nordeng 1983; O'Malley et al. 2019). The genetic relationship among resident and anadromous charr remains uncertain (Klemetsen 2010). Though differences among morphs have been proposed to be both genetic and plastic, historically there has been little evidence of genetic divergence among resident and anadromous charr (Nordeng 1983; Hindar et al. 1986; Moore et al. 2014; but see Chapter 2, 4).

A natural question then is what are the genetic relationships among anadromous, resident, and landlocked charr? Given their ecological and phenotypic differences, each morph is likely to experience different neutral and adaptive processes. Straying is expected to increase gene flow among anadromous populations in contrast to more isolated landlocked populations (Bernatchez et al. 1998; Moore et al. 2013; Boguski et al.

2016). Alternatively, residents may experience an intermediate level of genetic differentiation if they experience gene flow with sympatric anadromous morphs. Environmental differences between marine and freshwater environments are expected to lead to divergent selection between anadromous and non-anadromous (resident and landlocked) morphs. Indeed, significant adaptive genetic differentiation has been found between anadromous and resident forms of Atlantic Salmon (Perrier et al. 2013) as well as salt water and fresh water-inhabiting forms of Three-spined Stickleback (*Gasterosteus aculeatus*) (Deagle et al. 2012), Alewives (*Alosa pseudoharengus*) (Velotta et al. 2014), Killifish (*Lucania parva*) (Kozak et al. 2014), and *Galaxias maculatus* (Delgado et al. 2019, 2020). Genetic variation associated with anadromy (e.g., smoltification, migratory capacity, growth rate) may be selected against in non-anadromous morphs due to the energetic costs of smoltification and anadromy (Jonsson and Jonsson 1993). This is supported by the observation that, in comparison to anadromous populations, landlocked populations of Alewives (Velotta et al. 2014) and Arctic Charr (Staurnes et al. 1992) demonstrate reduced ability to osmoregulate in salt water. This reduced salinity tolerance in Arctic Charr is suggested to be due to a failure to increase expression of Na(+),K(+)-ATPase alpha1b mRNA in salt water (Bystriansky et al. 2007). Alternatively, genetic variation associated with anadromy may be lost stochastically in freshwater environments if it is no longer subject to positive selection but is unassociated with a fitness cost (relaxed selection)(Velotta et al. 2014). Retained genetic variation associated with anadromy could explain why landlocked Arctic Charr populations in Europe maintained a seasonal ability to osmoregulate in salt water similar to that observed in anadromous populations (Schmitz 1995). Investigation of the relative influence of these neutral and adaptive processes on the genetic relationships among anadromous, resident, and landlocked Arctic Charr is needed to understand how these morphs evolved.

In addition to contemporary adaptive and neutral processes, the evolutionary history of this species also potentially drives its remarkable polymorphism. During the Pleistocene, Arctic Charr occupied five glacial refugia (Atlantic, Siberian, Bering, Arctic, Acadian) (Brunner et al. 2001) and the glacial lineages descended from each refugium have accumulated genetic differences since their divergence (Brunner et al. 2001; Moore et al. 2015). However, it is unclear to what extent a population's glacial history has

influenced contemporary morph divergence as polymorphisms are observed across this species distribution in all five glacial lineages (e.g., allopatric blueback and silver charr in Maine, USA (Acadian lineage; Bernatchez et al. 2002), sympatric littoral and profundal morphs in Quebec (Arctic lineage; Power et al. 2009), sympatric large and small morphs in Alaska (probably Beringian lineage based on Moore et al. 2015; May-McNally et al. 2015b), sympatric planktivore, dwarf, piscivore, and abyssal morphs in Norway (Atlantic lineage; Østbye et al. 2020), sympatric and/or allopatric planktivorous, benthivorous, piscivorous, small-piscivorous, insectivorous in Russia (Siberian lineage, Jacobs et al. 2020). Though most charr populations demonstrate mtDNA haplotypes consistent with being founded by a single glacial lineage, secondary contact has occurred in several locations across this species Holarctic distribution (Brunner et al. 2001; Moore et al. 2015). Glacial lineage and colonization history may therefore critically influence contemporary genetic variation and shape morph evolution.

Colonization history as well as neutral and adaptive processes might also act to influence the genetic consistency of adaptive differentiation between morphs. Populations with a more recently shared ancestry are more likely to demonstrate parallel genetic differentiation, as has been observed in sticklebacks (Magalhaes et al. 2020). Genetic drift, particularly in isolated non-anadromous morphs, could also result in the loss of alleles which would otherwise be selected for, leading to a lack of genetic parallelism (Deagle et al. 2012). Genetic parallelism may also be reduced where multiple genetic pathways can be employed to achieve the same morph differentiation (Perrier et al. 2013). Alternatively, environmental conditions may vary among populations such that selective pressures differ across locations, resulting in a lack of genetic parallelism (Roesti et al. 2012). Whether anadromous, resident, and landlocked morphs of Arctic Charr demonstrate parallel genetic differentiation and at what "level" this occurs (e.g., at the level of the SNP, gene, paralog (gene family), or even gene expression level) remains largely untested. Therefore, the comparison of outlier loci between charr morphs will allow for the investigation of the genetic predictability of this morph differentiation.

Such an investigation of the genetic relationships among morphs is also critical to the conservation and management of this species. The anadromous charr morph is the basis of commercial, recreation, and subsistence fisheries across this species' distribution

(Klemetsen et al. 2003; Moore et al. 2013; Boguski et al. 2016). Many of these fisheries are managed by Indigenous peoples who have traditionally fished the anadromous morph for millennia (Kristofferson and Berkes 2005; Dempson et al. 2008; Roux et al. 2011; Snook et al. 2018). This morph continues to be an important source of nutrition in northern communities where its preservation is critical to prevent further food insecurity (Ford 2009). However, the anadromous morph is particularly vulnerable to climate change which is expected to increase temperatures and terrestrial primary productivity, selecting for residency in charr (Reist et al. 2006; Finstad and Hein 2012). Conservation of the anadromous morph therefore requires an understanding of how anadromous and non-anadromous populations are related.

Labrador is an ideal study location for assessing the relative importance of colonization history, neutral processes, and adaptation on the phenotypic and genotypic divergence of charr. Labrador was only recently deglaciated ~ 9000 years BP (Bryson et al. 1969; Occhietti et al. 2011) but multiple populations of both landlocked and anadromous charr have since become established (Van der Velden et al. 2015). This offers an ideal opportunity to investigate the character and consistency of the genetic underpinnings of early adaptive differentiation among morph types. Additionally, northern Labrador is one of the few locations in the world where charr from different glacial lineages (specifically the Arctic and Atlantic lineages) have come into secondary contact (Wilson et al. 1996; Brunner et al. 2001; Moore et al. 2015). The anadromous morph is the basis of an economically important commercial fishery based out of Nain as well as recreational and subsistence fisheries (Dempson et al. 2008). The contemporary presence of multiple glacial lineages as well as multiple geographically, ecologically, and morphologically differentiated forms of charr makes Labrador ideally suited to investigate the genetic underpinnings of morph differentiation.

In this thesis I therefore employed a number of genetic data to investigate for the presence and genetic characteristics of anadromous, resident, and landlocked morphs in Labrador, Canada. In Chapter 2, I used neutral microsatellite markers to uncover the genetic relationships among landlocked and anadromous populations of Arctic Charr from three drainages in the Torngat Mountains, Labrador. I detected genetic differences between small mature (putative resident) (see Fig.1.1 for image of small mature female,

see Fig.1.2 for image of small mature male from Hebron Brook, Labrador) and large mature anadromous (Fig.1.3) fish in a single lake (Ramah) as well as genetically distinguishable sympatric landlocked morphs. In Chapter 3 I used mtDNA to investigate the colonization history of Arctic Charr in Labrador and Newfoundland. I found evidence for extensive secondary contact and introgression between the Acadian, Arctic, and Atlantic lineages but no evidence that sympatric morphs were founded by different glacial lineages.

In Chapters 4-6 I used SNP data from a newly designed 87k SNP chip for Arctic Charr (Nugent et al. 2019). This chip was designed using charr samples from the Nauyuk, Tree River, and Fraser aquaculture strains as well as wild Icelandic charr (Nugent et al. 2019). This chip therefore captures genetic variation from multiple glacial lineages as wild Icelandic charr are all Atlantic lineage (Moore et al. 2015), the Nauyuk and Tree River aquaculture strains likely derive from populations founded by Arctic and/or Beringian glacial lineages (Moore et al. 2015). In addition, the Fraser River aquaculture strain is derived from a population in Labrador, Canada I found in Chapter 3 to have mtDNA consistent with both the Arctic and Atlantic lineages.

In Chapter 4, I used the SNP data generated from this chip to investigate the degree of genetic parallelism between sympatric size-differentiated morphs from three different drainages in northern Labrador. Though sympatric morphs consistently differed by length across replicate locations, there was evidence for only a few SNPs, genes, and paralogs demonstrating evidence of parallel genetic differences between morphs. In Chapter 5 I again used SNPs to investigate the degree of genetic parallelism between allopatric landlocked and anadromous morphs from five drainages across northern Labrador. I also assessed for genetic parallelism between size-differentiated morphs detected in two of these landlocked locations. Overall, I again found little evidence of genetic parallelism driving allopatric or sympatric genetic differentiation. However, several SNPs, genes, paralogs, and genomic regions, showed evidence for parallel differentiation between allopatric landlocked and anadromous morphs suggesting that such morph differentiation may be genetically consistent. In Chapter 6 I assessed the genetic diversities of and the pairwise genetic differences between anadromous, resident, and landlocked populations across Labrador using SNPs. As expected, landlocked and

resident populations had lower genetic diversities and higher genetic differentiation than anadromous populations. However, the stability of genetic diversity in landlocked populations through time, and the recent declines in genetic diversity in some anadromous populations indicate the potential vulnerability of some anadromous populations to environmental change. I also uncovered a correlation of genetic diversity with latitude in Labrador anadromous populations. This may be the result of the contemporary vulnerability of southern anadromous populations to climate change and the greater introgression between the Arctic and Atlantic lineage in northern Labrador. In Chapter 7 I investigate the genetic differences between sympatric morphs within Salmonidae and the processes driving and hindering this genetic differentiation. Here, I also assess the amount of genetic parallelism contributing to sympatric morph differentiation both within and across salmonid species. This body of work represents a major contribution to our understanding of Arctic Charr evolutionary biology and advocates for Arctic Charr joining the ranks of species such as sticklebacks, Darwin's Finches, and *Heliconius* butterflies as an ideal model for investigating the evolution of phenotypic diversity and incipient speciation in natural populations.

1.1 Statement of Co-Authorship

This thesis work includes five data chapters and a literature review. Three data chapters have been published while the remaining three chapters are intended to be submitted for publication. As the lead author for all published chapters, I conceptualized the project for each chapter, conducted lab work, field work, and data analyses, and primarily wrote the manuscripts. However, all chapters were conducted with the help of my co-authors who significantly contributed to this work by assisting with project design, sampling, lab work, data analyses, and editing/writing the manuscripts. The publications associated with each chapter are noted below:

Chapter 2:

Salisbury, S.J., Booker, C., McCracken, G.R., Knight, T., Keefe, D., Perry, R., and Ruzzante, D. E. 2018. Genetic divergence among and within Arctic char (*Salvelinus alpinus*) populations inhabiting landlocked and sea-accessible sites in Labrador, Canada. Canadian Journal of Fisheries and Aquatic Sciences. 75(8): 1256-1269.

Chapter 3:

Salisbury, S.J., McCracken, G.R., Keefe, D., Perry, R., and Ruzzante, D.E. 2019. Extensive secondary contact among three glacial lineages of Arctic Char (*Salvelinus alpinus*) in Labrador and Newfoundland. Ecology and Evolution. 9(4), 2031-2045.

Chapter 4:

Salisbury, S.J., McCracken, G.R., Perry, R., Keefe, D., Layton, K.K.S., Kess, T., Nugent, C.M., Leong, J.S., Bradbury, I.R., Koop, B.F., Ferguson, M.M., and Ruzzante, D.E. 2020. Limited genetic parallelism underlies recent, repeated incipient speciation in geographically proximate populations of an Arctic fish (*Salvelinus alpinus*). Molecular Ecology. 29(22): 4280-4294.

Chapter 5:

This chapter is unpublished, but authorship will be:

Salisbury, S.J., McCracken, G.R., Perry, R., Keefe, D., Layton, K.K.S., Kess, T., Nugent, C.M., Leong, J.S., Bradbury, I.R., Koop, B.F., Ferguson, M.M., and Ruzzante, D.E.

Chapter 6:

This chapter is unpublished.

Chapter 7:

This chapter is unpublished, but authorship will be:

Salisbury, S.J. and Ruzzante, D.E.

1.2 Figures

Fig.1.1 Small, mature female from Ramah Lake, Labrador. Photo by Daniel Ruzzante.

Fig.1.2 Small, mature male from Hebron Brook, Labrador. Photo by Sarah Salisbury.

Fig.1.3 Large, mature female from Ramah Lake, Labrador. Photo by Daniel Ruzzante.

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CHAPTER 2 - GENETIC DIVERGENCE AMONG AND WITHIN ARCTIC CHARR (*SALVELINUS ALPINUS*) POPULATIONS INHABITING LANDLOCKED AND SEA-ACCESSIBLE SITES IN LABRADOR, CANADA

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2.1 Abstract

Anadromous, resident, and landlocked Arctic Charr (*Salvelinus alpinus*) differentially experience drift and gene flow, making them ideal for studying incipient divergence. We investigated genetic divergence within and among charr occupying landlocked and sea-accessible sites in Labrador, Canada, using 11 microsatellites. Unlike anadromous charr, landlocked charr were highly genetically differentiated. Genetic subgroups were detected within landlocked and sea-accessible sites. Within Ramah Lake (a sea-accessible site containing two subgroups) one subgroup matured at a small size and both subgroups had equal proportions of males to females. These findings refute residency as a sneaker male tactic and instead suggest the presence of reproductively isolated resident and anadromous charr. Subgroups demonstrated equal frequencies of Atlantic and Arctic lineage mtDNA haplotypes, suggesting their genetic differences were not due to allopatry during the last glacial maximum. Our results are therefore consistent with the sympatric genetic divergence of resident and anadromous Arctic Charr morphs.

2.2 Introduction

Species which demonstrate phenotypically distinct "morphs" with a genetic component allow for the study of the factors driving incipient genetic divergence (Schluter 1996b; 2001). Probably no species demonstrates this polymorphism more clearly than Arctic Charr (*Salvelinus alpinus*) (Klemetsen 2010). Their phenotypic polymorphism, evolutionarily young populations, potential for sympatric and allopatric divergence, as well as secondary contact of glacial lineages make Arctic Charr an ideal

species for studying the influence of historical and contemporary processes on early phenotypic and genotypic divergence (Brunner et al. 2001). After the last glacial maximum (LGM), Arctic Charr colonized their current Holarctic distribution from multiple glacial refugia (Wilson et al. 1996; Brunner et al. 2001; Moore et al. 2015). Contemporarily, charr exist in both landlocked lakes that historically lost sea-access and in rivers and lakes with sea-access (Babaluk et al. 1997; Kapralova et al. 2011; May-McNally et al. 2015b). Differences in morphology, life history, behaviour and habitat use (Griffiths 1994; Jonsson and Jonsson 2001; Klemetsen 2010) have been observed both within and between landlocked populations and populations with sea-access. The source of this species' polymorphism has intrigued researchers for over 100 years (Robinson and Parsons 2002), but remains largely unresolved (Klemetsen 2010).

Most investigation into the source of the large phenotypic variation observed among charr, a phenomenon termed the "charr problem", has focused on landlocked lacustrine populations (Johnson 1980; Klemetsen et al. 2003). Genetic divergence among landlocked populations is high (Brunner et al. 1998; Adams et al. 2007; Shikano et al. 2015), but divergence between morphs within the same lake (when they occur) is often low, suggesting sympatric evolution of morphs (e.g., Gíslason et al. 1999; Alekseyev et al. 2009; May-McNally et al. 2015b but see Gomez-Uchida et al. 2008; Garduno-Paz et al. 2012 for exceptions). Different morphs are typically associated with distinct feeding habitats (e.g., littoral, pelagic, profundal zones) (e.g., Gíslason et al. 1999; Adams and Huntingford 2004; Eloranta et al. 2013). Consistent with their divergent feeding niches, morphs demonstrate differences in: isotope signatures (e.g., Power et al. 2009; Woods et al. 2013), parasite content (e.g., Conejeros et al. 2014; Knudsen et al. 2014), prey species composition (e.g., Knudsen et al. 2006; Woods et al. 2013) and morphological characters (e.g., Arbour et al. 2011; Garduno-Paz et al. 2012). The presence of morphs is more likely in larger, deeper, and more spatially complex lakes with few other fish species (Griffiths 1994; Riget et al. 2000; Power et al. 2009; for exceptions see Hindar and Jonsson 1982; O'Connell and Dempson 2002a; Power et al. 2009; Knudsen et al. 2016). Greater genetic divergence has also been associated with greater morphological and niche differences (Gíslason et al. 1999; Conejeros et al. 2014; Gordeeva et al. 2015). These observations are consistent with the hypothesis that Arctic Charr plasticity allows for

differential niche occupation, followed by reproductive isolation and sympatric genetic divergence (Skúlason et al. 1999; Snorrason and Skúlason 2004). The degree of genetic divergence between morphs is therefore likely to be contingent upon the magnitude and temporal stability of niche divergence (Skúlason et al. 1999; Parker et al. 2001; Snorrason and Skúlason 2004).

Charr found in sites with sea-access can also exhibit different morphs associated with niche occupation and feeding habitat, but unlike landlocked populations, this is primarily a function of anadromy (Loewen et al. 2009). Anadromous charr smoltify in spring after spending several years as freshwater parr (Radtke et al 1997; Boguski et al. 2016). Normally both smolts and adult charr feed in the marine environment during the summer and then return to fresh water in autumn, at which time adults spawn (Andrews and Lear 1956; LeDrew 1980; Dempson and Green 1985). The resulting fry hatch from eggs in spring (LeDrew 1980). Anadromous charr demonstrate low genetic divergence among populations, likely as a consequence of straying (Bernatchez et al. 1998; Moore et al. 2013; Boguski et al. 2016). A resident charr form which remains in fresh water year-round can sometimes co-occur with anadromous charr in sites with sea-access (Johnson 1976; Loewen et al. 2010). Anadromous and resident individuals differ in morphologies (e.g., Loewen et al. 2009; Moore et al. 2014), life histories (e.g., Nordeng 1983; Rikardsen et al. 2004), parasite exposure (Bouillon and Dempson 1989), and prey species consumption (Rikardsen et al. 2000).

The degree to which phenotypic differences between anadromous and resident charr are driven by plasticity or genetic differences remains uncertain. The greater lengths and faster growth observed in anadromous charr may be a function of higher quality food or more optimal temperatures experienced during the summer marine feeding session (Rikardsen et al. 2000; Loewen et al. 2010). Alternatively, residency/anadromy may represent different life-history trajectories (as determined by environmental conditions) where anadromous morphs delay maturation in favour of growth in contrast to resident morphs which mature early to the detriment of growth (Rikardsen et al. 2004). Residency has also been suggested as a sneaker-male tactic, where small, resident males maintain the colouration of immature parr which allows them to stealthily fertilize eggs of anadromous females who would otherwise prefer large

anadromous males as mates (Jonsson and Hindar 1982). Females should instead more readily undergo anadromy because in contrast to males, female reproductive output is more closely related with size which is maximized by anadromous feeding (Doucett et al. 1999; Loewen et al. 2010). This is supported by the highly male-skewed sex ratios observed in resident morphs (Loewen et al. 2010; Moore et al. 2014). Finally, anadromy and residency could be genetically determined traits maintained by frequency-based selection within a single population or by reproductive isolation (Moore et al. 2014). However, previous studies have found little to no support for evidence of genetic divergence among resident and anadromous charr (Hindar et al. 1986; Moore et al. 2014). The factors promoting residency and the genetic consequences of this phenotypic divergence from anadromous charr are therefore not well understood.

Labrador charr populations are ideally suited for studying the influence of historical and contemporary neutral processes on the genetic differences among charr forms. This is because Labrador charr are present in both landlocked and sea-accessible sites (van der Velden et al. 2015) and were historically founded by multiple glacial lineages (Wilson et al. 1996; Brunner et al. 2001; Moore et al. 2015). Here, we investigate the genetic divergence among and within charr populations existing in landlocked and sea-accessible sites. We predict that landlocked populations will be genetically similar to their geographically closest anadromous populations as both are assumed to be descended from a common anadromous ancestral population (Hindar et al. 1986; 1991). Among populations with sea-access we expect low genetic divergence and high gene flow due to the possibility of straying (Bernatchez et al. 1998; Moore et al. 2013; Boguski et al. 2016). Finally, we look to uncover evidence of genetic divergence within landlocked populations and within populations with sea-access.

2.3 Methods

2.3.1 Sampling

Arctic Charr samples were collected from three regions (Nackvak Fjord, Ramah Bay, and Saglek Fjord) in northern Labrador, Canada at a total of 10 locations (Fig.2.1). Eight sampling locations were accessible from the ocean; most were located at the mouth of watersheds draining into either the Nackvak or Saglek Fjord. However, one of the

sampling locations, Ramah Lake, is a freshwater lake, upstream of Ramah Bay. Fish were collected in Palmer River (Nachvak Fjord) in 2006 and 2007 and were combined for all analysis. Samples collected from Southwest Arm in 2007 and 2014 were instead treated separately for all analyses given the greater time difference and associated possibility for genetic differentiation. Two landlocked freshwater lakes (WP133 and WP132) were also sampled. These two lakes belong to the same watershed which drains into Saglek Fjord but are separated from the sea by multiple waterfalls which prevent access by anadromous charr (Anderson 1985). All charr sampled in these lakes are therefore lacustrine residents.

Samples were collected between 2006 and 2014 using electrofishing in the rivers (sea-accessible sites) and variably-sized standardized nylon monofilament gillnets (1.27 cm to 8.89 cm diagonal) at the two landlocked (WP132 and WP133) and one sea-accessible (Ramah Lake) lake sites. Fish were weighed, measured for fork length (FL) in mm, and assessed for sex and maturity. Pectoral fin clips were obtained and either immediately stored in 95% ethanol or stored dry (n = 1280).

2.3.2 DNA Extraction

Fin clips were digested at 55ºC for approximately eight hours using Proteinase K (Bio Basic Inc., Markham, ON, Canada). DNA was then extracted using a Multiprobe II plus liquid handling system (Perkin Elmer, Waltham, MA, USA) using a glassmilk protocol modified from Elphinstone et al. (2003).

2.3.3 Microsatellite Amplification and Genotyping

Eleven polymorphic microsatellite loci were selected for amplification: *Ssa407UOS* (Cairney et al. 2000), *OtsG83b* (Williamson et al. 2002), *Sco202*, *Sco206*, *Sco220* (Dehaan and Ardren 2005), *Sfo334Lav* (Perry et al. 2005), *SnaMSU06*, *SnaMSU09* (Rollins et al. 2009), *SfoC113*, *SfoD75*, (King et al. 2012), *Sco107* (Sewall Young, unpublished).

Samples were amplified using PCR (see Table S2.1 for reaction reagents and Table S2.2 for thermocycler conditions, Supporting Information), visualized using Li-COR 4200/4300 DNA Analyzers (Li-COR Biosciences, Lincoln, NE, USA), and genotyped

using SAGA Automated Microsatellite Software 3.3 (Li-COR Biosciences, Lincoln, NE, USA).

Scoring errors and null allele presence were assessed using MICROCHECKER 2.2.3 (van Oosterhout et al. 2004). Linkage disequilibrium was assessed using 10000 permutations and departures from Hardy-Weinberg equilibrium (HWE) were assessed using 1000000 Markov chain steps, and 100000 dememorization steps with Arlequin 3.5.1.3 (Excoffier and Lischer 2010). *P*-values were adjusted using the false discovery rate correction (Benjamini and Hochberg 1995).

2.3.4 Genetic Diversity Analyses

FSTAT (Goudet 2001) was used to estimate allele frequencies and allelic richness (A_R) per site and Arlequin was used to estimate observed (H_o) and expected (H_e) heterozygosity. $\widehat{F}_{ST}$s were estimated in MSA 4.05 using 100000 MCMC permutations (Dieringer and Schlötterer 2003). $\widehat{N}_e$ was estimated for each lake using LDNe (Waples and Do 2008) with and without first-generation migrants identified in GENECLASS2 (Piry et al. 2004) (see below for analysis details) to meet the assumption of closed subpopulations (Waples and Do 2008). For all LDNe analyses a P_{crit} (minimum allele frequency) of 0.02 was used as advised by Waples and Do (2010) since all lakes had a sample size > 25.

2.3.5 Migration Analyses

First generation migrants among populations were identified in GENECLASS2 with a Monte Carlo resampling method (Paetkau et al. 2004) of 1000 genotypes generated using a Bayesian analysis (Rannala and Mountain 1997) and a Type-I error of 0.01.

Contemporary migration rates among populations were estimated using BIMr (Faubet and Gaggiotti 2008) using 20 pilot runs, $1 * 10^6$ chains of burnin, and $2 * 10^5$ chains of sampling. We ran five replicates and likelihood convergence was confirmed by inspecting the program output. We report the results for only the run with the lowest mean likelihood following Palstra and Ruzzante (2010). Migration rates were considered

significant if the 95% confidence interval of the mean value over all runs had a lower bound greater than 0.

2.3.6 Within and Among Population Genetic Structure Analyses

Population structure was assessed with a principal coordinates analysis (PCoA) based on the linearized $\hat{F}_{ST}$s (Rousset 1997) using GenAlEx 6.501 (Peakall and Smouse 2006). Hierarchical population structure analyses were conducted using the admixture model, 10 replications, 200000 burn-in steps, and 500000 MCMC permutations with STRUCTURE 2.3.4 (Pritchard et al. 2000; Hubisz et al. 2009). The number of clusters (*K*) was estimated using the Evanno method (Evanno et al. 2005) and STRUCTURE HARVESTER (Earl and vonHoldt 2012). Replicates were aggregated using CLUMP 1.1.2 (Jakobsson and Rosenberg 2007) and visualized using DISTRUCT 1.1 (Rosenberg 2004).

Where K > 1 for a single sampling site, STRUCTURE *Q*-values were used to determine genetic subgroups. A_R, H_o, H_e, pairwise $\hat{F}_{ST}$s, and $\widehat{N}_e$s were estimated for genetic subgroups in the same manner described above. STRUCTURE-defined genetic subgroups were compared by sex (male or female) and maturity (mature or immature) using 2x2 χ^2 tests. A two-way ANOVA comparing fish length by maturity and genetic subgroup was conducted in R (R Core Team, 2013). Individuals were assigned to either one of two pure strains (Pure 0, Pure 1) or four hybrid classes (F1, F2, F1 backcrossed with a Pure 0 individual (0_Bx), F1 backcrossed with a Pure 1 individual (1_Bx)) using NewHybrids 1.1 (Anderson and Thompson 2002). Uniform priors, 100000 burnin steps, and 200000 sweeps were used for each run. Runs were repeated using different seed values and compared to ensure consistent results.

2.3.7 Mitochondrial Haplotype Amplification and Genotyping

Since both the sea-accessible site Ramah Lake, and the landlocked WP lakes each demonstrated K = 2 in the STRUCTURE analysis (see results below), the left domain region of the mitochondrial control region was sequenced to determine if these genetic subgroups corresponded with different glacial lineages. For Ramah Lake, the left domain of the control region was sequenced for 24 individuals from each genetic subgroup (as

determined by their STRUCTURE-assigned Q-value). For the WP lakes, 24 individuals (12 from each of the WP132 and WP133 lakes) were sequenced from each genetic subgroup (for a total of 48 individuals sequenced). MtDNA amplification and sequencing was conducted following Moore et al. (2015). In brief, the primers *Tpro2* (Brunner et al. 2001) and *SalpcrR* (Power et al. 2009) were used to amplify the entire control region using the thermocycler program and PCR reaction outlined in (Brown Gladden et al. 1995). A total of 512 bp of the left domain was sequenced using *Char3* (Power et al. 2009) at MacrogenUSA (Rockville, MD). Each unique haplotype detected was validated by resequencing a representative sample for each haplotype using *Tpro2*.

2.3.8 MtDNA analysis

Our control region sequences were aligned along with all control region haplotypes verified by Moore et al. (2015), and control region sequences for two outgroup species (Brook Trout (*Salvelinus fontinalis*) and Lake Trout (*Salvelinus namaycush*)) (for accession numbers see Table S2.3, Supporting Information) using GENEIOUS (10.0.9, www.geneious.com). A gap penalty of 5 was used and all other parameters were kept at default values. A tree was constructed using the PhyML (Guindon and Gascuel 2003) plugin in GENEIOUS to compare the phylogenetic relationships among the unique control region haplotypes identified from our samples with those haplotypes verified by Moore et al. (2015) and those of the outgroup species. We used the Nearest Neighbour Interchange topology search algorithm, the HKY85+I+G model, and calculated 1000 bootstraps for each node following Moore et al. (2015).

2.4 Results

2.4.1 Genetic Quality Control

A total of n = 1022 individuals were successfully amplified for at least 9 of 11 markers. No loci consistently demonstrated null alleles (nulls were only detected in *SnaMSU09* in SWAB, and *Ssa407UOS* in Southwest Arm (2014) and Ramah Lake) and we therefore retained all loci for subsequent analysis. Evidence of departures from HWE were found in 15 of 121 tests, but no individual locus consistently demonstrated departures from HWE over all sample sites (Table S2.4, Supporting Information).

Linkage disequilibrium was found between *OtsG83b* and *Sco107* in 8 of 10 sample sites (not in Schooner's Cove or North Arm). Analyses were therefore conducted with and without *OtsG83b* which was less successfully amplified than *Sco107*. Given that the STRUCTURE and PCoA results with and without *OtsG83b* were nearly identical, only the results including all loci will be discussed here (but see Fig.S2.1, S2.2 in Supporting Information for STRUCTURE and PCoA results without *OtsG83b*). No other locus pair demonstrated linkage disequilibrium.

2.4.2 Genetic Diversity

Genetic diversity estimates were lower in the two landlocked sampling sites (WP132, WP133) than the sites with sea-access. Allelic richness, A_R, varied between 5.30 in WP133 and 7.41 in Schooner's Cove (Table 2.1). Observed heterozygosity, H_o, varied between 0.73 in WP132 and WP133 and 0.85 in McCormick River. Expected heterozygosity, H_e, varied between 0.73 in WP132 and WP133 and 0.86 in Schooner's Cove.

Positive $\widehat{N}_e$s were obtained for 9 of 11 sampling sites (Schooner's Cove and Southwest Arm 2007 had negative values with or without the inclusion of migrants). $\widehat{N}_e$s varied between ~52 in WP132 and 990 in Palmer River when including migrants and between nearly 49 in WP132 and 1702 in Ramah Lake when excluding migrants. These values may be underestimates since positive $\widehat{N}_e$s were obtained for only 3 sites when the locus *OtsG83b* was removed from the analysis (Table S2.5, Supporting Information). $\widehat{N}_e$s for these three sites were an order of magnitude greater than those estimated when *OtsG83b* was included in the analysis.

2.4.3 Among Population Gene Flow

A total of 40 putative inter-population migrants were identified using GENECLASS2 (Table 2.2). All locations were the recipients of at least one putative migrant. Tor Bay, near the mouth of the Saglek Fjord (Fig.2.1) was the only location not to have contributed putative migrants. The analysis suggested migration both within and between locations within Nachvak fjord, Saglek fjord and Ramah Bay. The landlocked

lakes (WP132 and WP133) exchanged putative migrants only with sites in the nearby Saglek Fjord and not with sites in the other, more distant fjords.

The lakes WP132 and WP133 exhibited reciprocal significant gene flow (as estimated with BIMr) and, consistent with the GENECLASS analysis above, WP132 also exhibited gene flow into Southwest Arm (2014), one of the locations in Saglek Fjord (Fig.2.1; Table 2.3). Tor Bay was neither a source nor a recipient of significant gene flow. The remaining sampling locations with sea-access exhibited significant gene flow between both fjords and Ramah Bay.

2.4.4 Within and Among Population Genetic Structure

The initial STRUCTURE analysis supported $K = 2$ groups based on the Evanno et al. (2005) method (Fig.2.2, for Evanno and Ln probability plots see Fig.S2.3, Supporting Information) separating the ocean-access sites from the two landlocked sites. When considering only these two landlocked lakes, a second-level STRUCTURE analysis suggested K = 2 groups, but the observed sub-structuring was not consistent with sampling location (i.e., lake). Individuals from these two lakes were therefore subgrouped into WP132A, WP132B, WP133A, WP133B based on sampling location and assigned genetic group (WPA if STRUCTURE Q-score > 0.5, WPB if $Q < 0.5$). Among the sites with sea-access, a second-level STRUCTURE analysis indicated K = 4: Tor Bay and Ramah Lake were each found to be genetically distinguishable, and the remaining sites were grouped by fjord (Saglek or Nachvak) (Fig.2.2). Despite its overall distinctiveness, Ramah Lake demonstrated considerable admixture from both the Saglek and Nachvak groups. When considering only individuals caught in Ramah Lake in a third-level STRUCTURE analysis, there was evidence of K = 2 subgroups (Fig.2.2), henceforth denoted RamahA and RamahB. Individuals within Ramah Lake were assigned to a subgroup based on STRUCTURE Q-scores (RamahA if $Q > 0.5$, RamahB if $Q < 0.5$). Within the Nachvak Fjord, Palmer River was distinct from the other three sites, which did not differ genetically even with the use of location priors. Within the Saglek Fjord there was no evidence of further genetic differentiation except with the use of location priors which revealed the distinctiveness of North Arm from Southwest Arm (2007 and 2014).

These two temporal samples of Southwest Arm did not differ even with the use of location priors.

The PCoA of linearized F_{ST}s (for pairwise F_{ST}s and p-values see Table S2.6, S2.7, Supporting Information) supported the STRUCTURE results and indicated the genetic distinctiveness of the landlocked sites and to a lesser extent, of Tor Bay from the other sites with sea-access (Fig.2.3a). A second PCoA was conducted based on linearized F_{ST}s estimated using the genetic subgroups of Ramah Lake (RamahA, RamahB) and the landlocked sites (WP132A, WP132B, WP133A, WP133B). This PCoA revealed the considerable genetic differences between RamahA and RamahB and between the WPA and WPB groups (WP132A and WP133A vs. WP132B and WP133B) (Fig.2.3b).

2.4.5 Genetic subgroup characteristics

When considering only Ramah Lake individuals with known maturity status (n = 167), mature individuals were longer than immature individuals (mean lengths = 198.1 mm, 189.1 mm respectively, $F_{1,163} = 12.146$, $p \leq 0.001$), and RamahA individuals were longer than RamahB individuals (mean lengths = 316.6 mm, 125.7 mm respectively, $F_{1,163} = 208.043$, $p < 2 \times 10^{-16}$). Tukey's HSD post-hoc analysis was used to compare maturity/genetic groupings using a Bonferonni-corrected α-value ($\alpha = 0.05/6 = 0.0083$) after a significant interaction was observed between maturity and genetic group ($F_{1,163} = 7.17$, $p \leq 0.01$) (Fig.2.4a). Immature RamahA individuals were significantly longer than immature RamahB individuals (mean lengths = 275.8 mm, 113.9 mm respectively, $p < 1 \times 10^{-7}$), and mature RamahA individuals were significantly longer than mature RamahB individuals (mean lengths = 366.4 mm, 132.2 mm respectively, $p < 1 \times 10^{-7}$). Within RamahA mature individuals were longer than immature individuals ($p \leq 0.001$), but no difference was observed between mature and immature individuals in RamahB ($p \geq 0.686$). These results suggest one genetic subgroup (RamahA) is composed of small immature and large mature individuals, and the other genetic subgroup (RamahB) is composed of small individuals regardless of maturity.

When considering only individuals from WP132 and WP133 with known maturity status (n = 179), mature individuals were longer than immature individuals (mean lengths = 222.7 mm, 209.0 mm respectively, $F_{1,175} = 4.567$, $p \leq 0.034$), and WPB

individuals were longer than WPA individuals (mean length = 286.1, 182.4 mm respectively, $F_{1,175} = 40.349$, $p \leq 1.78 \times 10^{-9}$). Tukey's HSD post-hoc analysis was used to compare maturity/genetic groupings using a Bonferonni-corrected α-value ($\alpha = 0.05/6 = 0.0083$) after a significant interaction was observed between maturity and genetic group ($F_{1,175} = 6.351$, $p \leq 0.0126$) (Fig.2.4b). Immature WPB individuals were significantly longer than immature WPA individuals (mean lengths = 295.0 mm, 154.4 mm respectively, $p < 1 \times 10^{-7}$), but mature WPB and WPA individuals did not differ by length (mean lengths = 263.9 mm, 211.8 mm respectively, $p \geq 0.263$). Within WPA, mature individuals were marginally longer than immature individuals ($p \leq 0.011$), but no difference was observed in WPB mature and immature individuals ($p \geq 0.726$). Therefore, the relationships between size and maturity within the two genetic subgroups in the two landlocked lakes were not as clear as in Ramah Lake (Fig.2.4).

The NEWHYBRIDS analysis identified n = 13 putative hybrids (F1, F2, or backcross) between two genetic subgroups in Ramah Lake. F1, F2, and 1_Bx individuals demonstrated average *Q*-values (0.88, 0.68, 0.95, respectively) that were intermediate to those of pure breeding individuals (0.07 and 0.96 for Pure_0 and Pure_1 respectively) (Fig.2.4c). The average length of F1 individuals (295.0 mm) was intermediate to that for pure breeding individuals (130.4 mm and 327.6 mm Pure_0 and Pure_1, respectively). However, the lengths of the single F2 individual (99.0 mm) and single 1_Bx individual (408.0 mm) were not.

A total of n = 47 hybrids were identified between the two pure strains in the lakes WP132 and WP133. F1, F2, and 1_Bx individuals demonstrated average *Q*-values (0.80, 0.69, 0.89, respectively) and lengths (255.3 mm, 216.8 mm, 225.0 mm) that were intermediate to those for pure breeding individuals (*Q*-values = 0.13, 0.92, lengths = 284.6 mm, 161.8 mm for Pure_0 and Pure_1 respectively) (Fig.2.4d).

There was no significant difference in the number of males and females in each genetic subgroup in either Ramah Lake ($\chi^2_{(1)} = 0.07$, $p \geq 0.79$) or the landlocked lakes (WP132, WP133) ($\chi^2_{(1)} = 1.55$, $p \geq 0.21$). There was a significant difference in the number of mature and immature individuals in each genetic subgroup in both Ramah Lake ($\chi^2_{(1)} = 8.99$, $p \leq 0.01$) and the WP lakes ($\chi^2_{(1)} = 19.80$, $p \leq 8.61 \times 10^{-6}$). This was primarily due to an excess of mature individuals in RamahB (70.4% of individuals were

mature) and an excess of immature individuals in WPB (29.6% of individuals were mature). There was little difference between H_o, H_e, and A_R in RamahA and RamahB and $\widehat{N}_e$s were indeterminate (negative) for both subgroups (Table 2.4). In contrast, in the landlocked lakes, H_o, H_e, A_R, and $\widehat{N}_e$s were higher in WP132A and WP133A than in WP132B and WP133B. We estimated $\widehat{N}_e$ for each genetic subgroup after eliminating individuals identified as potential migrants (migrants between genetic subgroups within Ramah Lake and within WP132 and WP133, and between these and all other sampling sites were re-estimated in GENECLASS2). GENECLASS2 results when Ramah Lake, WP132, and WP133 were split into genetic subgroups (Table S2.8, Supporting Information) were similar to those GENECLASS2 results reported above.

The most common haplotype identified in both RamahA and RamahB was the Atlantic haplotype, ATL01, followed by the Arctic haplotype, ARC19 or ARC24, (which couldn't be differentiated due to the SNP distinguishing these two haplotypes lying outside the 512 bp region that was sequenced) (Fig.S2.4 a,b, Supporting Information). RamahA included one individual with the ARC22 haplotype, whereas RamahB included one individual with the ATL04 haplotype. The STRUCTURE *Q*-values were not significantly different between those individuals with Arctic haplotypes and those with Atlantic haplotypes ($T_{46} = -0.717$, $p = 0.477$), suggesting that the neutral genetic differences between subgroups were not associated with different glacial lineages.

Three new haplotypes were identified in individuals from WP132 and WP133 (Fig.S2.4 c,d, Supporting Information). These three haplotypes were all associated with the Atlantic lineage and formed a monophyletic clade (Fig.2.5). The most common haplotype, ATL23, was found in both the WPA and WPB genetic subgroups. Two additional haplotypes, ATL24 and ATL25, were each observed in a single individual in WP133 and both belonged to the WPA genetic subgroup. No Arctic haplotype was observed in either of the landlocked lakes (WP132 and WP133).

2.5 Discussion

2.5.1 Population Structure Among Landlocked Lakes

Multiple lines of evidence suggest that the landlocked lakes are genetically isolated and experience a high degree of drift. These lakes were associated with the

highest pairwise $\hat{F}_{ST}$s, and lowest migration rates, H_o, H_e, A_R, and $\widehat{N}_e$s. Furthermore, the greatest genetic split detected by STRUCTURE was between these lakes and all other sites. The prevalence of previously undocumented Atlantic mtDNA haplotypes in the WP lakes may have been the result of fixation of rare haplotypes due to drift (in contrast to the nearby Ramah Lake which contained Atlantic haplotypes previously observed in European populations (Moore et al. 2015)). The high waterfalls separating these lakes from all other sites likely form a significant barrier to gene flow, resulting in the isolation and increased genetic drift experienced by these populations.

These results are consistent with similar observations in landlocked lakes within Maine (Bernatchez et al. 2002), Alaska (May-McNally et al. 2015b) Iceland, the British Isles, and Scandinavia (Wilson et al. 2004; Shikano et al. 2015) where lakes were highly genetically differentiated but unrelated by distance suggesting the importance of drift. Alternatively, several cases have been reported of highly genetically differentiated landlocked populations clustered together by geographic region (Hindar et al. 1986; Primmer et al. 1999) or for which differentiation correlates with overland distance (Kapralova et al. 2011), suggesting the lingering genetic influence of colonization history. The detection of migration between the WP lakes and anadromous populations within the Saglek Fjord (the most geographically proximate anadromous populations to these lakes) could therefore be a result of the common ancestry of these populations rather than contemporary migration.

However, the STRUCTURE and PCoA results did not suggest WP132 and WP133 were more closely related to anadromous populations within the Saglek Fjord than to anadromous populations in Nachvak Fjord or Ramah Bay. This is contrary to our hypothesis that the Saglek anadromous populations are descendants of the ancestral anadromous charr that founded the populations in the WP lakes. It is possible that these lakes were colonized by a population that is genetically different from the one that founded the Saglek Fjord anadromous populations. Alternatively, the low effective sizes observed in these lakes may have contributed to their increased drift and genetic differentiation, thereby eroding the genetic relatedness with modern Saglek anadromous populations. Landlocked populations are thus currently genetically distinguishable and

isolated from anadromous populations and require a unique conservation strategy separate from that for anadromous populations.

2.5.2 Population Structure Among Sea-Accessible Sites

In contrast to the landlocked populations, anadromous populations exhibited low genetic divergence from each other as indicated by the PCoA and some of the STRUCTURE results, even with the use of location priors. The genetic similarities between anadromous populations are likely the result of straying (Bernatchez et al. 1998; Moore et al. 2013; Boguski et al. 2016; Santaquiteria et al. 2016) which is supported by the high migration rates observed between anadromous populations using both GENECLASS2 and BIMr. However, the eventual genetic differentiation of most sampling locations as well as the genetic grouping of Saglek and Nachvak sites in the second level of the hierarchical STRUCTURE analysis suggest that straying is not enough to erode the genetic differentiation caused by natal homing. This is consistent with the low dispersal observed in Arctic Charr in Labrador (Bernatchez et al. 1998). Additionally, the significant migration rates between sampling locations within fjords and bays (i.e., within Saglek, Nachvak, and Ramah Bay) were on average higher than between these three regions, suggesting that straying is limited by geography and occurs largely exclusively among locations within fjords but rarely among them. LeDrew (1980) found that anadromous charr present in Labrador rivers further south than those studied here rarely migrated more than 65 km from their natal river. This distance exceeds that between Nachvak and Saglek Fjords but not between each of these fjords and Ramah Bay. Ramah Bay may therefore be an important steppingstone that facilitates connectivity between anadromous populations inhabiting these two fjords.

In contrast to this general trend of low genetic divergence among anadromous populations, PCoA and STRUCTURE revealed the Tor Bay population to be uniquely genetically distinguishable. This distinction is likely the result of drift due to Tor Bay's geographic isolation.

2.5.3 Population Structure Within Landlocked Lakes

The finding of genetic subgroups within the lakes WP132 and WP133 is consistent with similar observations of within-lake genetic divergence in charr elsewhere (e.g., Volpe and Ferguson 1996; May-McNally et al. 2015b). The lack of difference in sex ratio between WPA and WPB as well as the observation of mature males and females in each genetic subgroup, suggests that these genetic subgroups have the capacity to be reproductively isolated (Moore et al. 2014). Alternatively, the greater number of immature relative to mature individuals sampled in WPB may be a result of sampling bias. This is particularly likely if WPA and WPB occupy different habitats, as the gillnets deployed to capture samples from these lakes may have missed WPB adults. Furthermore, the consistent observation of lowered genetic diversity in WPB relative to WPA over multiple metrics suggests the subgroups are reproductively isolated since introgression would erode differences in allelic richness and heterozygosity (Gomez-Uchida et al. 2008). The low diversity observed in WPB may have also caused this genetic subgroup to experience greater drift (Gomez-Uchida et al. 2008), resulting in its greater divergence from all other populations in comparison to WPA. The reduced genetic diversities observed in WPB are intriguing since they suggest that WPB may be a divergent offshoot population of WPA which occurred via niche partitioning or expansion (Knudsen et al. 2006). Regardless, the support for genetic subgrouping in these lakes coupled with the finding that this differentiation is not associated with lake location suggests the waterfall separating these two lakes (WF6 in Fig.2.1) is likely an incomplete barrier to gene flow (in disagreement with Anderson 1985).

We suspect that the genetic subgroups observed in the WP lakes are likely to have arisen sympatrically since all site/genetic groupings within the WP lakes are more closely related to each other than to any other sampled population (see e.g., Volpe and Ferguson 1996; Gíslason et al. 1999; May-McNally et al. 2015b). The observation of only Atlantic lineage haplotypes in the WP lakes was surprising (given that this is the furthest north Atlantic haplotypes have been observed in Labrador) but is consistent with the sympatric divergence of WPA and WPB. These results confirm that the observed neutral genetic divergence within these lakes is not due to secondary contact of glacial lineages.

However, a more recent allopatric divergence followed by secondary contact and hybridization, cannot be ruled out.

2.5.4 Population Structure Within Sea-Accessible Sites

The RamahA and RamahB genetic subgroups distinguished by STRUCTURE and collected from the same gill nets in Ramah Lake, are respectively consistent with the anadromous and resident life history morphs often observed in charr populations with sea-access. In accordance with the observation that anadromous individuals achieve greater lengths than residents (Loewen et al. 2010), RamahA individuals were longer than RamahB individuals. Within RamahB, immature and mature individuals were small and demonstrated no difference in length whereas in RamahA immature individuals were smaller than mature individuals. Interestingly, both mature and immature RamahA individuals were respectively larger than RamahB mature and immature individuals. This may reflect the potential for smolts to undertake migration (and experience the associated rapid growth) for multiple years before maturation (Klemetsen et al. 2003; Boguski et al. 2016) resulting in anadromous charr achieving a large size before maturation. Additionally, the greater number of mature relative to immature individuals sampled in RamahB is consistent with the earlier maturation of residents in comparison to anadromous individuals (Loewen et al. 2010). While we were unable to conduct a microchemistry analysis to confirm the anadromy and residency of RamahA and RamahB, respectively, the observed interaction between length and maturity for these two genetic subgroups supports their proposed life histories. Length is also the trait most likely to be affected by a resident versus anadromous life history (e.g., Jonsson and Hindar 1982; Jonsson and Jonsson 2001; Loewen et al. 2009).

There was little evidence for the hypothesis that small mature residents are mostly males employing a “sneaker-male” mating strategy to avoid the fitness costs of anadromy (Jonsson and Hindar 1982; Jonsson and Jonsson 2001; Loewen et al. 2010). Male-skewed sex ratios have previously been observed in resident charr leading to the suggestion that residents and anadromous individuals form a single population (Nordeng 1983; Loewen et al. 2010; Moore et al. 2014). Moore et al. (2014) found male-biased sex ratios in resident charr and a lack of genetic differentiation between resident and anadromous

charr in south-eastern Baffin Island, Nunavut. The lack of sex-ratio skew in RamahA and RamahB, as well as the presence of mature females in the resident genetic group RamahB supports the potential for these two genetic subgroups to exist as independent populations. In the field we observed a slight difference in egg development stage between females of the two groups. The small and presumed "resident" females exhibited translucent eggs that seemed ready to be extruded while the eggs in the large anadromous females appeared to be in an earlier development stage. This suggests these genetic subgroups may spawn at slightly different times leading to a pattern of isolation by time (Hendry and Day 2005). This prezygotic reproductive barrier has also been observed in European populations of charr (Westgaard et al. 2004; Corrigan et al. 2011; Garduño-Paz et al. 2012).

While we acknowledge that the lack of age data limits the interpretability of our results, the genetic divergence observed between RamahA and RamahB is unlikely to be a result of age differences or a cohort effect. We can assume that a range of ages were collected for both genetic subgroups due to the presence of both mature and immature individuals in each subgroup. The genetic divergence observed within Ramah Lake is also not likely to be the result of different cohorts since there was no genetic difference detected in another site with sea-access (Southwest arm) despite 7 years between sampling events.

The low levels of genetic divergence between these genetic subgroups suggest that they are more likely the result of sympatric divergence than from the erosion of allopatric divergence from introgression (Magnusson and Ferguson 1987; Garduño-Paz et al. 2012). Furthermore, RamahB is genetically closest to RamahA (based on pairwise linearized $\hat{F}_{ST}$s) but RamahA is genetically more similar to several other anadromous populations. Thus, our results for these subgroups within Ramah Lake can be interpreted as the outcome of sympatric divergence followed by reproductive isolation of the resident subgroup causing its increased drift. Anadromous individuals instead would be expected to maintain a genetic association with other anadromous populations due to straying (Moore et al. 2013; Boguski et al. 2016). Additionally, the lack of significant difference in the Q-values associated with Atlantic and Arctic haplotypes suggest that the observed neutral genetic divergence between RamahA and RamahB is not due to allopatric

divergence from the LGM. The sympatric divergence of anadromous and resident forms has been supported in other salmonid species in which low, but significant genetic divergence has been observed between these forms (e.g., Atlantic Salmon (*Salmo salar*) (Verspoor and Cole 1989; Vuorinen and Berg 1989), Brown Trout (*Salmo trutta*) (Skaala and Naevdal 1989), Sockeye Salmon (*Onchorhynchus nerka*) (Wood and Foote 1996)). To our knowledge however, our results represent the first time genetic divergence has been observed between anadromous and resident forms of Arctic Charr.

Although we do not know what drives this sympatric genetic divergence between resident and anadromous forms in Ramah Lake, potential drivers include differences in salinity (Moore et al. 2016), temperature (Chavarie et al. 2010), predation (including human harvesting) (Moore et al. 2014; 2016), prey (Rikardsen et al. 2000), and parasites (Bouillon and Dempson 1989) between the summer feeding habitats occupied by resident and anadromous charr. Additionally, Ramah Lake's greater distance from the ocean (~ 10 km) may have also increased the fitness of residents relative to that of anadromous individuals (Finstad and Hein 2012). Such an increase in fitness associated with the resident niche could result in selection against hybridization between resident and anadromous charr and drive the sympatric genetic divergence between morphs.

2.5.5 Conclusions

Our results suggest that like other salmonids, sympatric anadromous and resident forms of Arctic Charr can be genetically distinguishable from each other. The identification and comparison of additional anadromous populations with varying levels of genetic divergence between morphs is required to determine the factors driving the occurrence of residents and this genetic divergence. Furthermore, while glacial lineage did not play a role in neutral genetic differentiation within Ramah Lake and the WP lakes, our results suggest a potentially elaborate colonization of Labrador by the Arctic and Atlantic lineages. While beyond the scope of this study, an investigation of the relationship between glacial lineage and morph manifestation is warranted. Labrador is an excellent study site to answer such questions given that it has two glacial lineages (Brunner et al. 2001; Moore et al. 2015) and contains populations inhabiting both landlocked and sea-accessible sites which demonstrate genetic substructuring (this study).

Anadromous Arctic Charr form important commercial, recreational, and subsistence fisheries (Klemetsen et al. 2003; Moore et al. 2013; Boguski et al. 2016) but are sensitive to temperature changes and are therefore threatened by climate change (Power et al. 2000; Moore et al. 2016). An understanding of the genetic relationship between anadromous charr and residents and the factors driving this is critical for the conservation of this species.

2.6 Acknowledgements

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2.7 Tables

Table 2.1 Genetic characteristics of Arctic Charr (*Salvelinus alpinus*) collected from 10 locations in Labrador, Canada. A_R is allelic richness, H_O is observed heterozygosity, H_E is expected heterozygosity, $\widehat{N}_e$ is effective size estimate, CI is confidence interval.

Sampling Location	Sampling Year	Code	Latitude, Longitude	N	H_O	H_E	A_R	$\widehat{N}_e$	Jackknife CI	$\widehat{N}_e$ (no migrants)	Jackknife CI
Schooner's Cove	2006	SC	59° 05′ 48″, 63° 30′ 34″	11	0.80	0.86	7.41	-16.8	(-25.4, ∞)	-11.6*	(-19.4, ∞)
McCormick River	2006	MR	59° 01′ 01″, 63° 44′ 39″	73	0.85	0.85	7.21	660.4	(72.1, ∞)	728.5	(75.4, ∞)
Ivatik Cove	2007	IC	59° 00′ 29″, 63° 44′ 16″	88	0.82	0.84	7.00	264.2	(52.4, ∞)	282.4	(54.5, ∞)
Palmer River	2006/2007	PR	58° 57′ 00″, 63° 52′ 55″	152	0.84	0.85	6.97	940.5	(131.2, ∞)	1702.2	(150.9, ∞)
Ramah Lake	2014	RH	58° 50′ 29″, 63° 28′ 39″	170	0.83	0.84	7.26	797.3	(50.6, ∞)	1172.6	(54.4, ∞)
Tor Bay	2007	TB	58° 26′ 55″, 62° 48′ 36″	73	0.80	0.80	5.77	122	(37.6, ∞)	106.0	(33.3, ∞)
Southwest Arm	2007	SA07	58° 29′ 07″, 63° 27′ 47″	75	0.78	0.82	6.77	-705.2	(72.5 ∞)	-782.9*	(69.7, ∞)
Southwest Arm	2014	SA14	58° 29′ 07″, 63° 27′ 47″	133	0.80	0.83	6.75	130.1	(32.5, ∞)	124.7	(31.0, ∞)
North Arm	2007	NA	58° 32′ 54″, 63° 27′ 38″	54	0.79	0.79	6.28	989.6	(51.9, ∞)	583.4	(44.2, ∞)
WP132	2014	WP132	58° 16′ 49″, 63° 58′ 09″	80	0.73	0.73	5.39	52.2	(22.9, 236.8)	48.9	(22.2, 188.1)
WP133	2014	WP133	58° 16′ 18″, 64° 01′ 53″	113	0.73	0.73	5.30	85.0	(20.7, ∞)	84.1	(20.8, ∞)

* Negative $\widehat{N}_e$ may be due to a large population size or insufficient sample size (Waples and Do 2010).

Table 2.2 Putative origin of Arctic Charr (*Salvelinus alpinus*) caught at 10 sampling locations in Labrador, Canada, calculated using GENECLASS2. SC - Schooner's Cove, MR - McCormick's River, IC - Ivatik Cove, PR - Palmer River, RH – Ramah Lake, TB - Tor Bay, SA07 - Southwest Arm sampled in 2007, SA14 - Southwest Arm sampled in 2014, NA - North Arm.

		Nachvak					Saglek					
	Into/From	SC	MR	IC	PR	RH	TB	SA07	SA14	NA	WP132	WP133
Nachvak	SC	8	1			1			1			
	MR		71			1		1				
	IC			84	1	1				2		
	PR		2		147	1			2			
	RH		1	1	1	164		1	2			
Saglek	TB						70	1	1			1
	SA07		1					73	1			
	SA14	1		1		1		1	127	1	1	
	NA		1			2		1		49	1	
	WP132								1		78	1
	WP133									1	1	111

Table 2.3 Migration rates between 10 sampling locations of Arctic Charr (*Salvelinus alpinus*) in Labrador, Canada, calculated using BIMr. Values that had a 95% confidence interval with a lower bound greater than 0 are bolded. SC - Schooner's Cove, MR - McCormick's River, IC - Ivatik Cove, PR - Palmer River, RH – Ramah Lake, TB - Tor Bay, SA07 - Southwest Arm sampled in 2007, SA14 - Southwest Arm sampled in 2014, NA - North Arm.

		Nachvak					Saglek					
	Into/From	**SC**	**MR**	**IC**	**PR**	**RH**	**TB**	**SA07**	**SA14**	**NA**	**WP132**	**WP133**
Nachvak	**SC**	**1**	$1.26x10^{-10}$	$1.26x10^{-10}$	$1.25x10^{-10}$	$1.26x10^{-10}$	$1.26x10^{-10}$	$1.26x10^{-10}$	$1.25x10^{-10}$	$1.25x10^{-10}$	$1.26x10^{-10}$	$1.26x10^{-10}$
	MR	**0.103915**	**0.272601**	**0.275005**	0.046068	**0.039305**	0.007458	**0.051128**	**0.122509**	**0.066957**	0.007739	0.007315
	IC	**0.083691**	**0.171282**	**0.412021**	0.01689	**0.076684**	0.006222	**0.085985**	**0.101248**	0.033863	0.005961	0.006154
	PR	**0.050804**	**0.061236**	**0.051546**	**0.634799**	**0.052226**	0.006962	**0.05341**	**0.036289**	**0.042833**	0.005506	0.004389
	RH	**0.162232**	**0.128562**	0.013084	0.024047	**0.506526**	0.005292	**0.074845**	**0.057082**	0.019856	0.004528	0.003947
Saglek	**TB**	$2.05x10^{-9}$	$2.04x10^{-9}$	$2.03x10^{-9}$	$2.04x10^{-9}$	$2.03x10^{-9}$	**1**	$2.05x10^{-9}$	$2.04x10^{-9}$	$2.06x10^{-9}$	$2.03x10^{-9}$	$2.05x10^{-9}$
	SA07	**0.156965**	**0.120029**	0.010319	0.007272	0.018715	0.011734	**0.170391**	**0.244224**	**0.233164**	0.015769	0.011419
	SA14	**0.111969**	**0.102142**	0.006772	0.005686	0.02092	0.008619	**0.153351**	**0.315069**	**0.245076**	**0.024613**	0.005783
	NA	$1.51x10^{-9}$	$1.51x10^{-9}$	$1.52x10^{-9}$	$1.52x10^{-9}$	$1.51x10^{-9}$	$1.51x10^{-9}$	$1.51x10^{-9}$	$1.52x10^{-9}$	**1**	$1.51x10^{-9}$	$1.50x10^{-9}$
	WP132	0.010604	0.005192	0.005303	0.005373	0.00518	0.005368	0.012921	0.007902	0.006603	**0.53205**	**0.403504**
	WP133	0.006697	0.003769	0.003926	0.004888	0.004146	0.003813	0.005698	0.005155	0.00452	**0.328077**	**0.629311**

Table 2.4 Characteristics of Arctic Charr (*Salvelinus alpinus*) genetic subgroups (as determined by STRUCTURE Q-values) identified within Ramah Lake and within the lake sites (WP132 and WP133) in Labrador, Canada. I is immature, M is mature, A_R is allelic richness, H_O is observed heterozygosity, H_E is expected heterozygosity, $\widehat{N}_e$ is effective size estimate, CI is confidence interval. Note that some individuals had unknown sex and/or maturity, therefore N ≠ I♂ + I♀ + M♂ + M♀.

Genetic Subgroup	N	I♂	I♀	M♂	M♀	H_O	H_E	A_R	$\widehat{N}_e$	Jackknife CI	$\widehat{N}_e$ (no migrants)	Jackknife CI
RamahA	**61**	18	13	17	10	0.84	0.84	13.42	-167.1*	(83.0, ∞)	-160.8	(80.9, ∞)
RamahB	**109**	11	18	46	23	0.83	0.82	13.05	-196.4*	(88.3, ∞)	-196.4	(88.3, ∞)
WP132A	**50**	10	19	11	5	0.76	0.76	9.09	262.3	(48.7, ∞)	214.4	(42.9, ∞)
WP132B	**30**	13	7	4	3	0.68	0.64	5.52	31.8	(10.3, ∞)	34.7	(12.8, ∞)
WP133A	**83**	19	9	24	20	0.76	0.75	9.08	207.7	(36.6, ∞)	247.5	(38.2, ∞)
WP133B	**30**	14	4	4	5	0.67	0.65	5.95	23.5	(8.3, 3121.7)	23.5	(8.3, 3121.7)

* Negative $\widehat{N}_e$ may be due to a large population size or insufficient sample size (Waples and Do 2010).

2.8 Figures

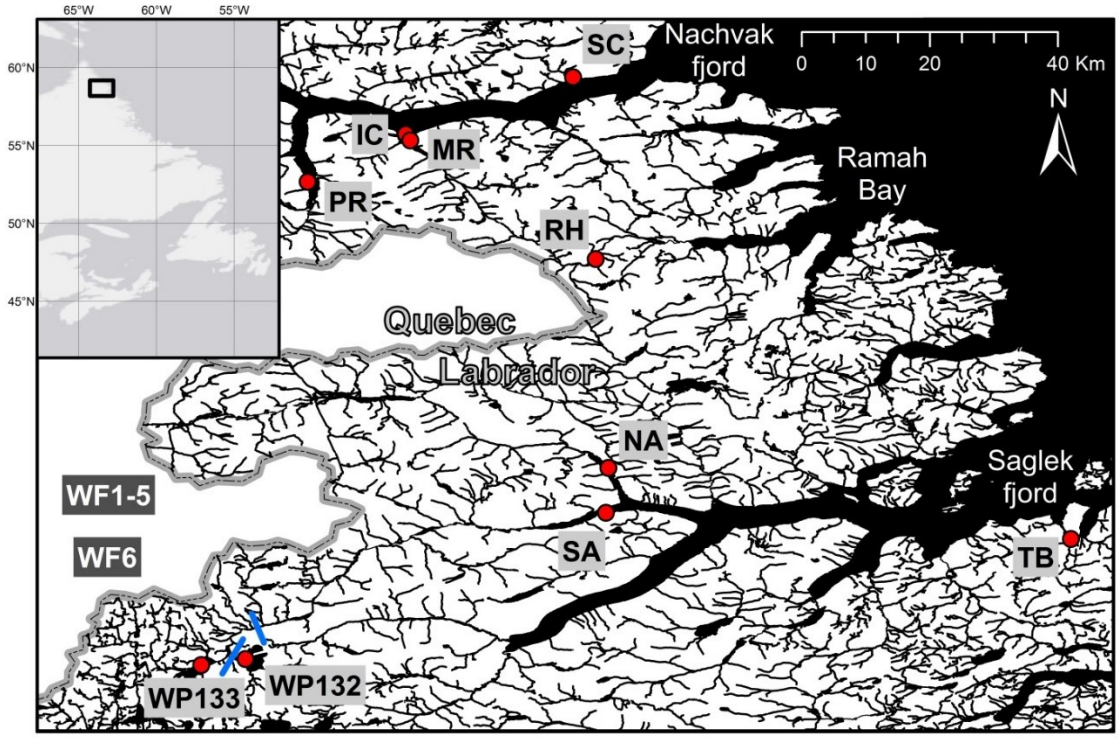


Fig.2.1 Ten sampling sites for Arctic Charr (*Salvelinus alpinus*) in Labrador, Canada: Schooner's Cove (SC), McCormick's River (MR), Ivatik Cove (IC), Palmer River (PR), Ramah Lake (RH), Tor Bay (TB), Southwest Arm (SA), North Arm (NA), Lakes WP132, and WP133. Blue lines indicate waterfalls that are complete barriers (Anderson 1985). Waterfalls 1-5 (WF1-5) are downstream from both lakes WP132 and WP133, waterfall 6 (WF6) is immediately downstream from WP132 and prevents migration to WP133 (Anderson 1985). Map created using ArcGIS (ESRI) with data from Geogratis (Natural Resources Canada).

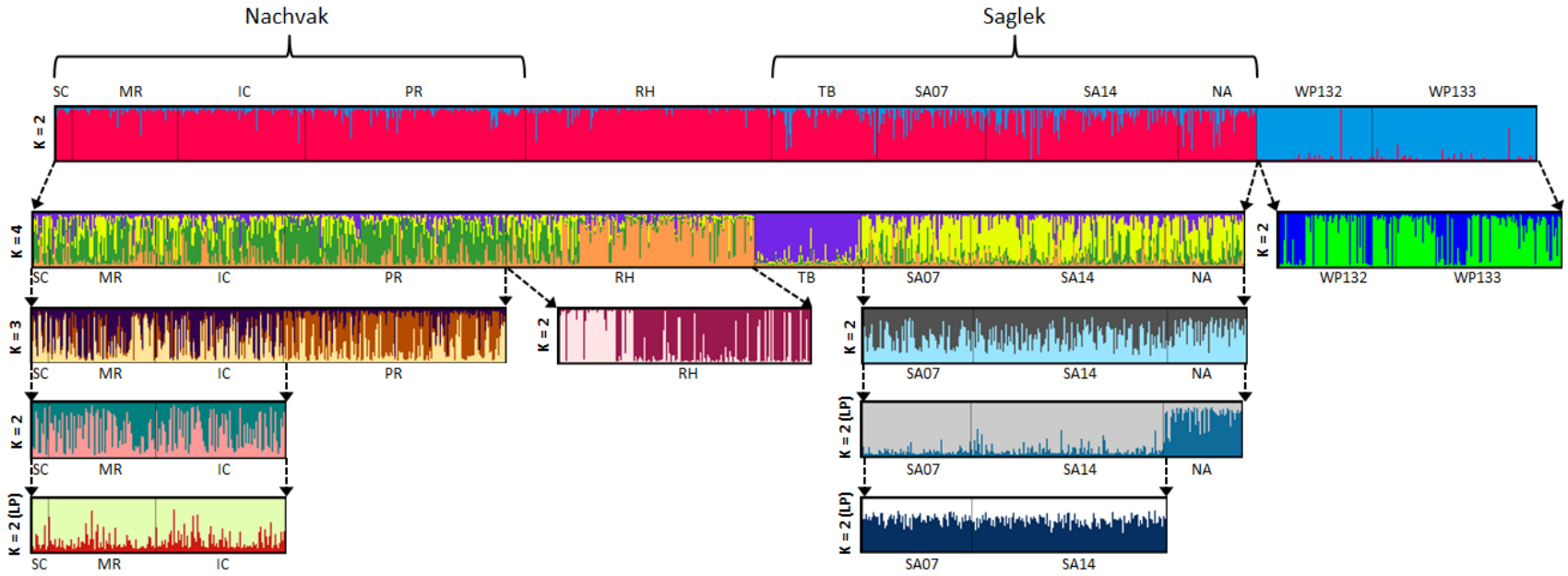


Fig.2.2 Hierarchical STRUCTURE analysis of Arctic Charr (*Salvelinus alpinus*) characterized at 11 loci. Samples were collected from 10 sampling locations in Labrador, Canada: Schooner's Cove (SC), McCormick's River (MR), Ivatik Cove (IC), Palmer River (PR), Ramah Lake (RH), Tor Bay (TB), Southwest Arm 2007 (SA07), Southwest Arm 2014 (SA14), North Arm (NA), WP132, and WP133. The number of genetic groupings (K) is indicated for each analysis. LP indicates the use of location priors.

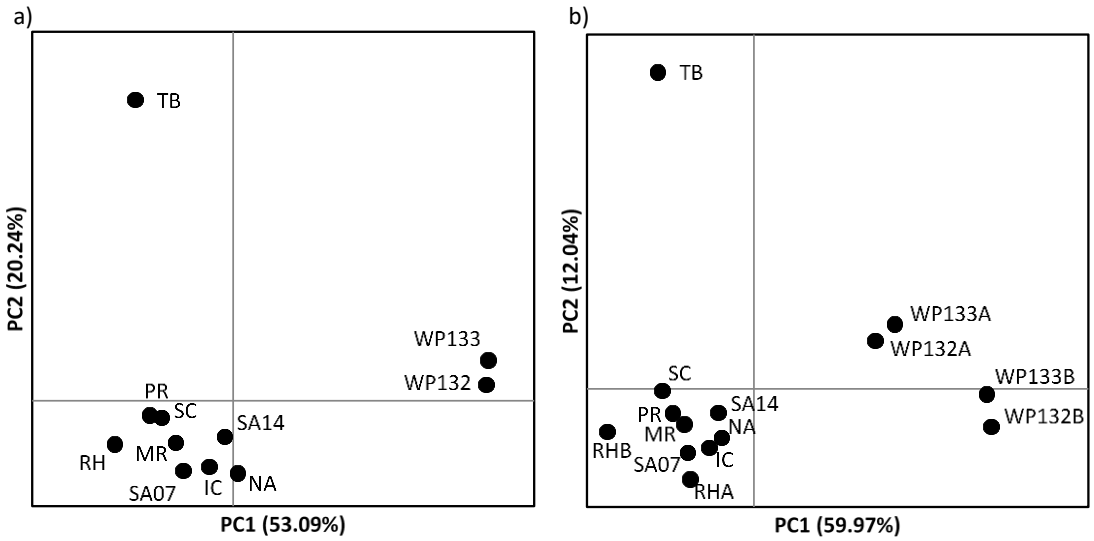


Fig.2.3 Principal Coordinates Analysis of Arctic Charr (*Salvelinus alpinus*) characterized at 11 loci and grouped according to a) 10 sampling locations, b) STRUCTURE-defined genetic groups (including substructure within Ramah Lake and within WP132 and WP133). Sampling locations include: Schooner's Cove (SC), McCormick's River (MR), Ivatik Cove (IC), Palmer River (PR), Ramah Lake (RH, with genetic subgroups RHA and RHB), Tor Bay (TB), Southwest Arm 2007 (SA2007), Southwest Arm 2014 (SA14), North Arm (NA), WP132 (with genetic subgroups WP132A and WP132B), and WP133 (with genetic subgroups WP133A and WP133B).

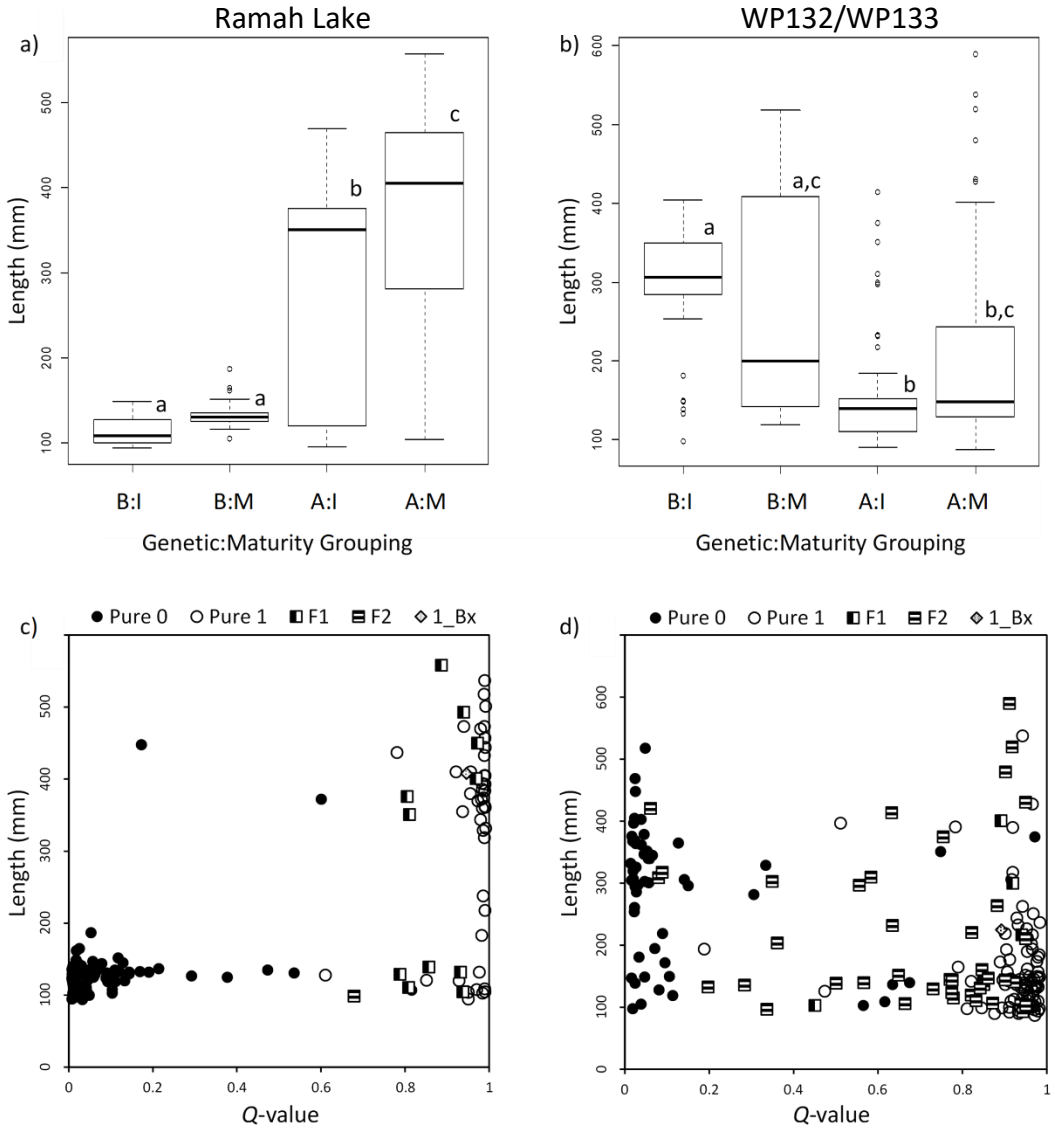


Fig.2.4 Length of mature (M) and immature (I) Arctic Charr (*Salvelinus alpinus*) in each of two genetic subgroups defined by STRUCTURE *Q*-values (A if $Q > 0.5$, B if $Q < 0.5$) in a) Ramah Lake and b) WP132 and WP133 in Labrador, Canada. Common letters indicate non-significant Tukey's HSD test based on a Bonferroni-corrected α-value (0.5/6=0.00 83). Length (mm) versus STRUCTURE *Q*-value by NEWHYBRID-assigned admixture classification (two pure parental strains (Pure 0, Pure 1), F1 hybrid, F2 hybrid, F1 backcross with Pure 0 individual (0_Bx), F1 backcross with Pure 1 individual (1_Bx)) in c) Ramah Lake and d) WP132 and WP133.

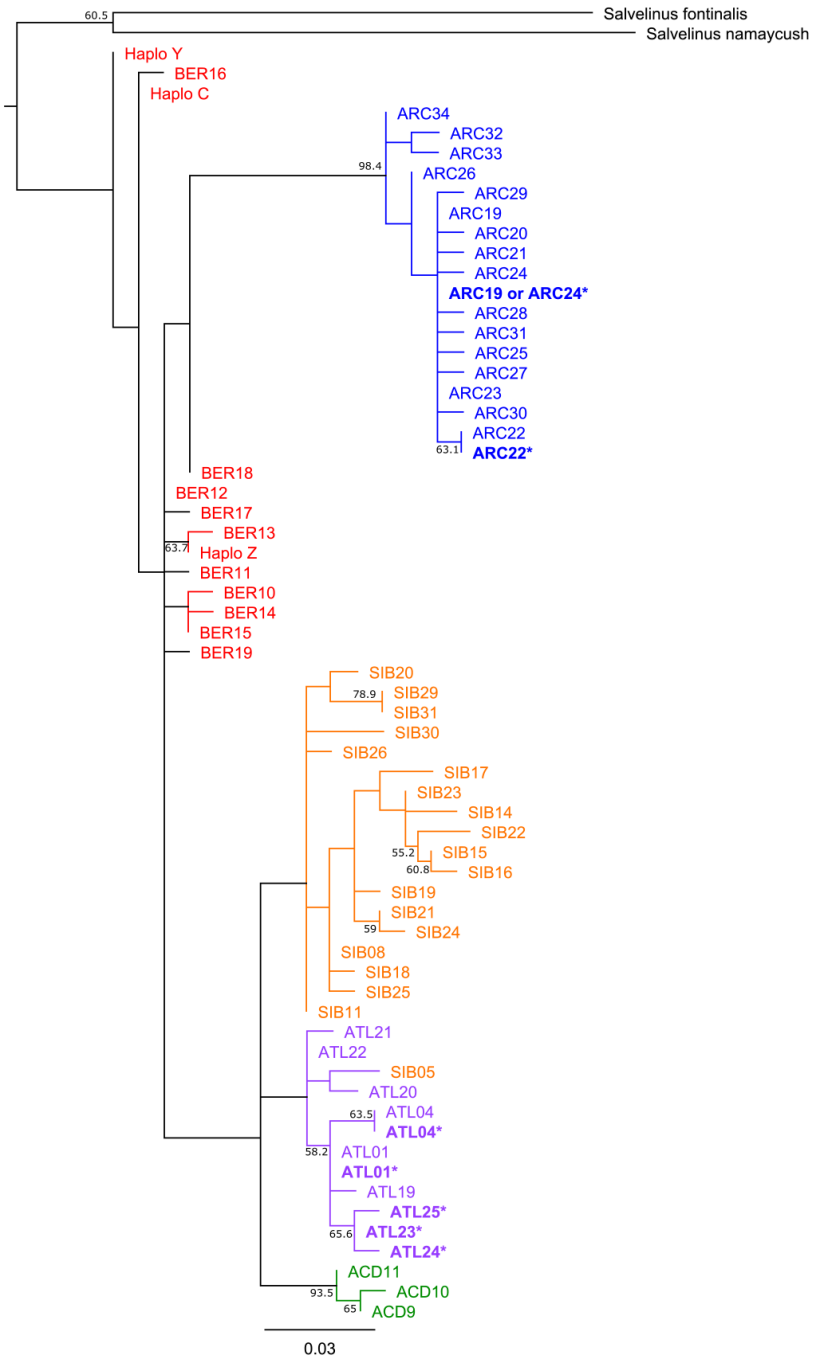


Fig.2.5 Maximum likelihood phylogenetic tree of Arctic Charr (*Salvelinus alpinus*) haplotypes of the mtDNA control region. Tree was generated using PhyML (Guindon and Gascuel 2003) with 1000 bootstrap replicates. Those bootstrap values greater than 50% are shown on the tree. Haplotypes are colour-coordinated by lineage as designated in Moore et al. (2015): blue - Arctic, red - Bering, orange - Siberia, purple - Atlantic, green, - Acadian. Those haplotypes sequenced in this study are bolded and starred.

2.9 Supporting Information

Table S2.1 PCR reaction reagents for amplification of Arctic Charr (*Salvelinus alpinus*) genetic samples collected from Labrador, Canada. *SfoC113* and *Ssa707UOS* were fluorescently labeled primers, all other microsatellites were amplified using m13.

PCR reaction using m13	**PCR reaction using fluorescently-labeled primers**
2.3 µL RNAse free water	2.35 µL RNAse free water
0.5 µL 10X reaction buffer (Bio Basic Inc., Markham, Ontario)	0.5 µL 10X reaction buffer (Bio Basic Inc., Markham, Ontario)
0.5 µL (2 mM) $MgSO_4$	0.5 µL (2 mM) $MgSO_4$
0.5 µL (0.2 mM) dNTPs (Bio Basic Inc., Markham, Ontario)	0.5 µL (0.2 mM) dNTPs (Bio Basic Inc., Markham, Ontario)
0.05 µL (0.01 mM) m13 tagged primer	0.05 µL (0.01 mM) fluorescently-labeled primer (700 nm or 800 nm fluorescence)
0.05 µL (0.1 mM) untagged primer	0.05 µL (0.1 mM) untagged primer
0.05 µL (0.1 mM) m13 fluorescent tag (700 nm or 800 nm fluorescence)	0.25 U TSG Polymerase (Qiagen Inc., United States)
0.25 U TSG Polymerase (Qiagen Inc., United States)	1.0 µL (< 5 ng) DNA
1.0 µL (< 5 ng) DNA	
5 µL Total Volume	**5 µL Total Volume**

Table S2.2 Thermocycling conditions for amplification of Arctic Charr (*Salvelinus alpinus*) genetic samples collected from Labrador, Canada. *Sco107*, *SnaMSU06*, *Sco202*, *SfoC113*, *Ssa407UOS*, *and Sco220* were amplified using the 55°C annealing program. *SnaMSU09* using the 57°C annealing program. *Sfo334* was amplified using the 60°C annealing program. *OtsG83b*, *Sco206*, and *SfoD74* were amplified using the touchdown program.

	55°C Annealing Thermocycle	**57°C Annealing Thermocycle**	**60°C Annealing Thermocycle**		**Touchdown Thermocycle**
	95°C - 5 min	95°C - 5 min	95°C - 5 min		95°C - 15 min
X 35 Cycles	95°C - 45 s	95°C - 45 s	95°C - 45 s	X 15 Cycles	95°C - 45 s
	55°C - 45 s	57°C - 45 s	60°C - 45 s		65°C - 45 s
	72°C - 45 s	72°C - 45 s	72°C - 45 s		72°C - 45 s
	72°C - 5 min	72°C -5 min	72°C - 5 min	X 18 Cycles	95°C -45 s
					55°C - 45 s
					72°C - 45 s
					72°C - 5 min

Table S2.3 GenBank accession numbers for all control region haplotypes used in mitochondrial analysis.

Haplotype name	Original source	GenBank accession number
ARC19	Alekseyev et al. 2009	EU310899
ARC20	Moore et al. 2015	KC907317
ARC21	Moore et al. 2015	KC907318
ARC22	Moore et al. 2015	KC907319
ARC23	Moore et al. 2015	KC907320
ARC24	Moore et al. 2015	KC907321
ARC25	Moore et al. 2015	KC907322
ARC26	Moore et al. 2015	KC907323
ARC27	Moore et al. 2015	KC907324
ARC28	Moore et al. 2015	KC907325
ARC29	Moore et al. 2015	KC907326
ARC30	Moore et al. 2015	KC907327
ARC31	Moore et al. 2015	KC907328
ARC32	Moore et al. 2015	KR011244
ARC33	Moore et al. 2015	KR011243
ARC34	Ayers 2010	KR011245
BER10	Alekseyev et al. 2009	EU310900
BER11	Alekseyev et al. 2009	EU310901
BER12	Alekseyev et al. 2009	EU310902
BER13	Alekseyev et al. 2009	EU310903
BER14	Moore et al. 2015	KR011246
BER15	Moore et al. 2015	KR011247
BER16	Ayers 2010	KR011248
BER17	Ayers 2010	KR011250
BER18	Ayers 2010	KR011251
BER19	Moore et al. 2015	KR011249
HaploC	Taylor et al. 2008	KR011254
HaploY	Taylor et al. 2008	KR011253
HaploZ	Taylor et al. 2008	KR011252
SIB5	Brunner et al. 2001	AF298013
SIB8	Brunner et al. 2001	AF298016
SIB11	Alekseyev et al. 2009	EU310907
SIB12	Alekseyev et al. 2009	EU310908
SIB14	Alekseyev et al. 2009	EU310910
SIB15	Alekseyev et al. 2009	EU310911
SIB16	Alekseyev et al. 2009	EU310912
SIB17	Alekseyev et al. 2009	EU310913
SIB18	Alekseyev et al. 2009	EU310914
SIB19	Alekseyev et al. 2009	EU310915
SIB20	Alekseyev et al. 2009	EU310916
SIB21	Alekseyev et al. 2009	EU310917
SIB22	Alekseyev et al. 2009	EU310918

Continued on next page

Table S2.3 Continued.

Haplotype name	Original source	GenBank accession number
SIB23	Alekseyev et al. 2009	EU310919
SIB24	Alekseyev et al. 2009	EU310920
SIB25	Alekseyev et al. 2009	EU310921
SIB26	Alekseyev et al. 2009	EU310922
SIB29	Alekseyev et al. 2009	EU310925
SIB30	Alekseyev et al. 2009	EU310926
SIB31	Moore et al. 2015	KR011255
ATL1	Brunner et al. 2001	AF297991
ATL4	Brunner et al. 2001	AF297994
ATL19	Moore et al. 2015	KR011258
ATL20	Moore et al. 2015	KR011261
ATL21	Moore et al. 2015	KR011257
ATL22	Moore et al. 2015	KR011256
ATL23	New	
ATL24	New	
ATL25	New	
ACD9	Alekseyev et al. 2009	EU310898
ACD10	Moore et al. 2015	KR011259
ACD11	Moore et al. 2015	KR011260
S. fontinalis	Kesken, E. (GenBank only)	HQ167705
S. namaycush	Taylor et al. 2008	KT362731

Table S2.4 Hardy-Weinberg equilibrium results from Arlequin 3.5.1.3 (Excoffier and Lischer 2010) for 11 loci amplified with Arctic Charr (*Salvelinus alpinus*) collected from 10 sampling sites in Labrador, Canada. SC - Schooner's Cove, MR - McCormick's River, IC - Ivatik Cove, PR - Palmer River, RH – Ramah Lake, TB - Tor Bay, SA07 - Southwest Arm sampled in 2007, SA14 - Southwest Arm sampled in 2014, NA - North Arm.

HWE?	**Sampling Site**										
Loci	**SC**	**MR**	**IC**	**PR**	**TB**	**RH**	**SA07**	**SA14**	**NA**	**WP132**	**WP133**
SnaMSU09	YES	YES	YES	YES	YES	YES	YES	YES	YES	YES	YES
OtsG83b	YES	YES	YES	YES	YES	YES	YES	YES	YES	YES	YES
Sco107	YES	YES	YES	YES	YES	YES	YES	YES	YES	YES	YES
Sco206	YES	YES	YES	YES	YES	YES	YES	NO	YES	YES	YES
SnaMSU06	YES	YES	YES	YES	YES	YES	YES	YES	YES	YES	YES
SfoD75	YES	YES	NO	YES	YES	YES	YES	YES	YES	NO	YES
Sco202	YES	YES	YES	YES	YES	YES	YES	YES	YES	YES	NO
Sfo334	YES	NO	NO	NO	YES	YES	NO	YES	NO	NO	NO
SfoC113	YES	YES	YES	YES	YES	YES	YES	YES	YES	YES	YES
Ssa407UOS	YES	YES	YES	YES	YES	NO	NO	NO	YES	YES	YES
Sco220	YES	YES	YES	YES	YES	YES	YES	YES	YES	YES	NO

Table S2.5 $\widehat{N}_e$ estimated using LDNe (Waples and Do 2008) for Arctic Charr (*Salvelinus alpinus*) in 10 sampling locations collected from Labrador, Canada, using 10 microsatellite loci (i.e., without *OtsG83b*).

Population	$\widehat{N}_e$	Jackknife CI	$\widehat{N}_e$ (no migrants)	Jackknife CI
Schooner's Cove	-14.4	(-23.0, ∞)	-10.2	(-16.5, ∞)
McCormick River	-263.8	(-5345.8, ∞)	-202.3	(-906.0, ∞)
Ivatik Cove	-465.9	(1162.2, ∞)	-431.3	(1348.7, ∞)
Palmer River	-593	(10717.4 ∞)	-522.8	(-14697.8, ∞)
Ramah Lake	-178.7	(-260.8, ∞)	-178.9	(-266.4, ∞)
Tor Bay	1099.1	(234.3, ∞)	993.6	(239.0, ∞)
Southwest Arm 2007	-137.8	(-255.7 ∞)	-132.6	(-250.0, ∞)
Southwest Arm 2014	-4601.1	(694.0, ∞)	-4342.2	(777.1, ∞)
North Arm	-144.3	(-398.0, ∞)	-145.2	(-388.8, ∞)
WP132	105.9	(68.6, 199.5)	101.3	(67.1, 181.4)
WP133	781.1	(259.0, ∞)	688.3	(239.1, ∞)

* Negative $\widehat{N}_e$ may be due to a large population size or insufficient sample size (Waples and Do 2010).

Table S2.6 Pairwise $\hat{F}_{ST}$s (below main diagonal) and p-values $\hat{N}_e$ (above main diagonal) estimated using MSA (Dieringer and Schlötterer 2003) for Arctic Charr (*Salvelinus alpinus*) in 10 sampling locations collected from Labrador, Canada, using 11 microsatellite loci. Sampling locations include: Schooner's Cove (SC), McCormick's River (MR), Ivatik Cove (IC), Palmer River (PR), Tor Bay (TB), Southwest Arm 2007 (SA2007), Southwest Arm 2014 (SA14), North Arm (NA), WP132, WP133, and Ramah Lake (RH).

	SC	MR	IC	PR	TB	SA07	SA14	NA	WP132	WP133	RH
SC	0	0.00269	0.0012	0.00002	0.00001	0.00015	0.00011	0.00001	0.00001	0.00001	0.00001
MR	0.01013	0	0.00878	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001
IC	0.0123	0.00175	0	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001
PR	0.01854	0.01403	0.02228	0	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001
TB	0.05447	0.05603	0.06689	0.05762	0	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001
SA07	0.01889	0.01611	0.02199	0.02722	0.06531	0	0.00466	0.00001	0.00001	0.00001	0.00001
SA14	0.01814	0.01713	0.01832	0.02978	0.05835	0.00214	0	0.00001	0.00001	0.00001	0.00001
NA	0.03514	0.02154	0.01681	0.03476	0.07315	0.01697	0.01226	0	0.00001	0.00001	0.00001
WP132	0.08476	0.07482	0.06536	0.09215	0.12038	0.07788	0.06072	0.06622	0	0.00008	0.00001
WP133	0.08532	0.07917	0.06986	0.08998	0.11677	0.08129	0.06234	0.06563	0.00535	0	0.00001
RH	0.02436	0.01928	0.02746	0.01969	0.06329	0.02122	0.02924	0.04147	0.10544	0.10835	0

Table S2.7 Pairwise $\hat{F}_{ST}$s (below main diagonal) and p-values $\hat{N}_e$ (above main diagonal) estimated using MSA (Dieringer and Schlötterer 2003) for Arctic Charr (*Salvelinus alpinus*) in 10 sampling locations. Three of these sampling locations (WP132, WP133, Ramah Lake) are further divided into genetic subgroups based on STRUCTURE Q-values (subgroups were designated A and B for each location). Samples were collected from Labrador, Canada, and amplified using 11 microsatellite loci. Sampling locations include: Schooner's Cove (SC), McCormick's River (MR), Ivatik Cove (IC), Palmer River (PR), Tor Bay (TB), Southwest Arm 2007 (SA07), Southwest Arm 2014 (SA14), North Arm (NA), WP132, WP133, and Ramah Lake (RH).

	SC	MR	IC	PR	TB	SA07	SA14	NA	WP132A	WP132B	WP133A	WP133B	RamahA	RamahB
SC	0	0.00233	0.00105	0.00001	0.00001	0.00014	0.00012	0.00001	0.00001	0.00001	0.00001	0.00001	0.00016	0.00001
MR	0.01013	0	0.00904	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001
IC	0.0123	0.00175	0	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001
PR	0.01854	0.01403	0.02228	0	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001
TB	0.05447	0.05603	0.06689	0.05762	0	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001
SA07	0.01889	0.01611	0.02199	0.02722	0.06531	0	0.00457	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001
SAA14	0.01814	0.01713	0.01832	0.02978	0.05835	0.00214	0	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001
NA	0.03514	0.02154	0.01681	0.03476	0.07315	0.01697	0.01226	0	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001
WP132A	0.07013	0.06206	0.05609	0.08266	0.10745	0.06839	0.0509	0.05575	0	0.00001	0.00004	0.00001	0.00001	0.00001
WP132B	0.14178	0.11894	0.10522	0.12899	0.16559	0.11921	0.10247	0.11274	0.05879	0	0.00001	0.03024	0.00001	0.00001
Wp133A	0.0758	0.07034	0.06184	0.08291	0.10632	0.07384	0.05466	0.05747	0.00904	0.04734	0	0.00001	0.00001	0.00001
WP133B	0.13138	0.11514	0.10487	0.12041	0.1571	0.11569	0.09761	0.10544	0.05111	0.00693	0.03515	0	0.00001	0.00001
RamahA	0.01676	0.01297	0.01629	0.01493	0.07127	0.01656	0.0182	0.02882	0.07217	0.11507	0.07275	0.1125	0	0.00001
RamahB	0.04097	0.0345	0.04489	0.03446	0.06933	0.03487	0.04524	0.0601	0.11974	0.1709	0.12676	0.16867	0.03272	0

Table S2.8 Migrants between 14 genetic/site groupings of Arctic Charr (*Salvelinus alpinus*), collected from Labrador, Canada, calculated using GENECLASS2, specifically: Schooner's Cove (SC), McCormick's River (MR), Ivatik Cove (IC), Palmer River (PR), Ramah Lake (RH, with genetic subgroups RHA and RHB), Tor Bay (TB), Southwest Arm 2007 (SA2007), Southwest Arm 2014 (SA14), North Arm (NA), WP132 (with genetic subgroups WP132A and WP132B), and WP133 (with genetic subgroups WP133A and WP133B).

		Nachvak						Saglek							
	Into/From	SC	MR	IC	PR	RHA	RHB	TB	SB	SA	NA	WP132 A	WP132 B	WP133 A	WP133 B
Nachvak	SC	8	1			1				1					
	MR		72						1						
	IC		1	84	1						2				
	PR		1		147	2				2					
	RHA		1			60									
	RHB						109								
Saglek	TB							70	1	1				1	
	SA07		1			1			72	1					
	SA14	1		1			1		1	127	1	1			
	NA		1				1		2		50				
	WP132A									1		48		1	
	WP132B												28	1	1
	WP133A										1			82	
	WP133B														30

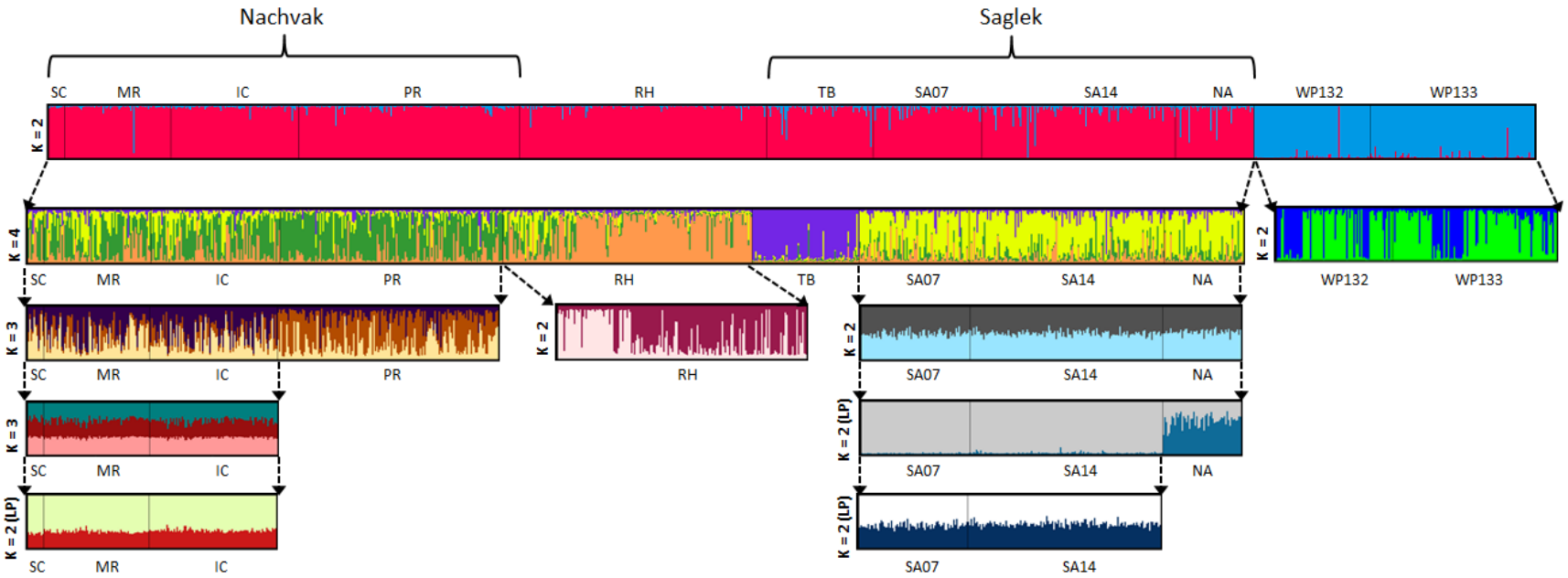


Fig.S2.1 Hierarchical STRUCTURE analysis of Arctic Charr (*Salvelinus alpinus*) characterized at 10 loci (i.e., excluding *OtsG83b*). Samples were collected from 10 sampling locations in Labrador, Canada: Schooner's Cove (SC), McCormick's River (MR), Ivatik Cove (IC), Palmer River (PR), Ramah Lake (RH), Tor Bay (TB), Southwest Arm 2007 (SA07), Southwest Arm 2014 (SA14), North Arm (NA), WP132, and WP133. The number of genetic groupings (K) is indicated for each analysis. LP indicates the use of location priors.

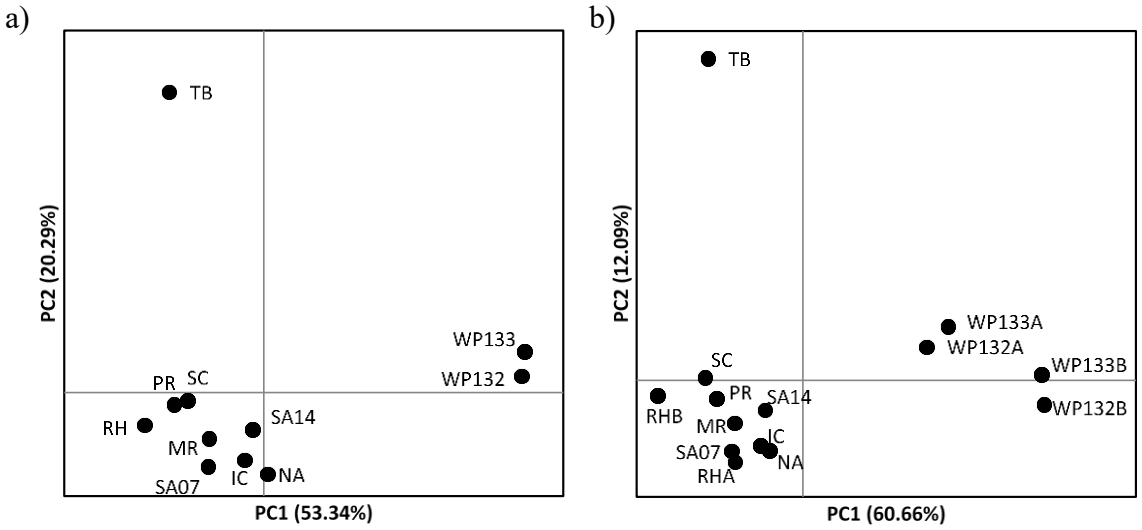


Fig.S2.2 Principal Coordinates Analysis Arctic Charr (*Salvelinus alpinus*) characterized at 10 loci (i.e., excluding *OtsG83b*) and grouped according to a) 10 sampling locations, b) STRUCTURE-defined genetic groups (including substructure within Ramah Lake and within WP132 and WP133). Sampling locations include: Schooner's Cove (SC), McCormick's River (MR), Ivatik Cove (IC), Palmer River (PR), Ramah Lake (RH, with genetic subgroups RHA and RHB), Tor Bay (TB), Southwest Arm 2007 (SA2007), Southwest Arm 2014 (SA14), North Arm (NA), WP132 (with genetic subgroups WP132A and WP132B), and WP133 (with genetic subgroups WP133A and WP133B).

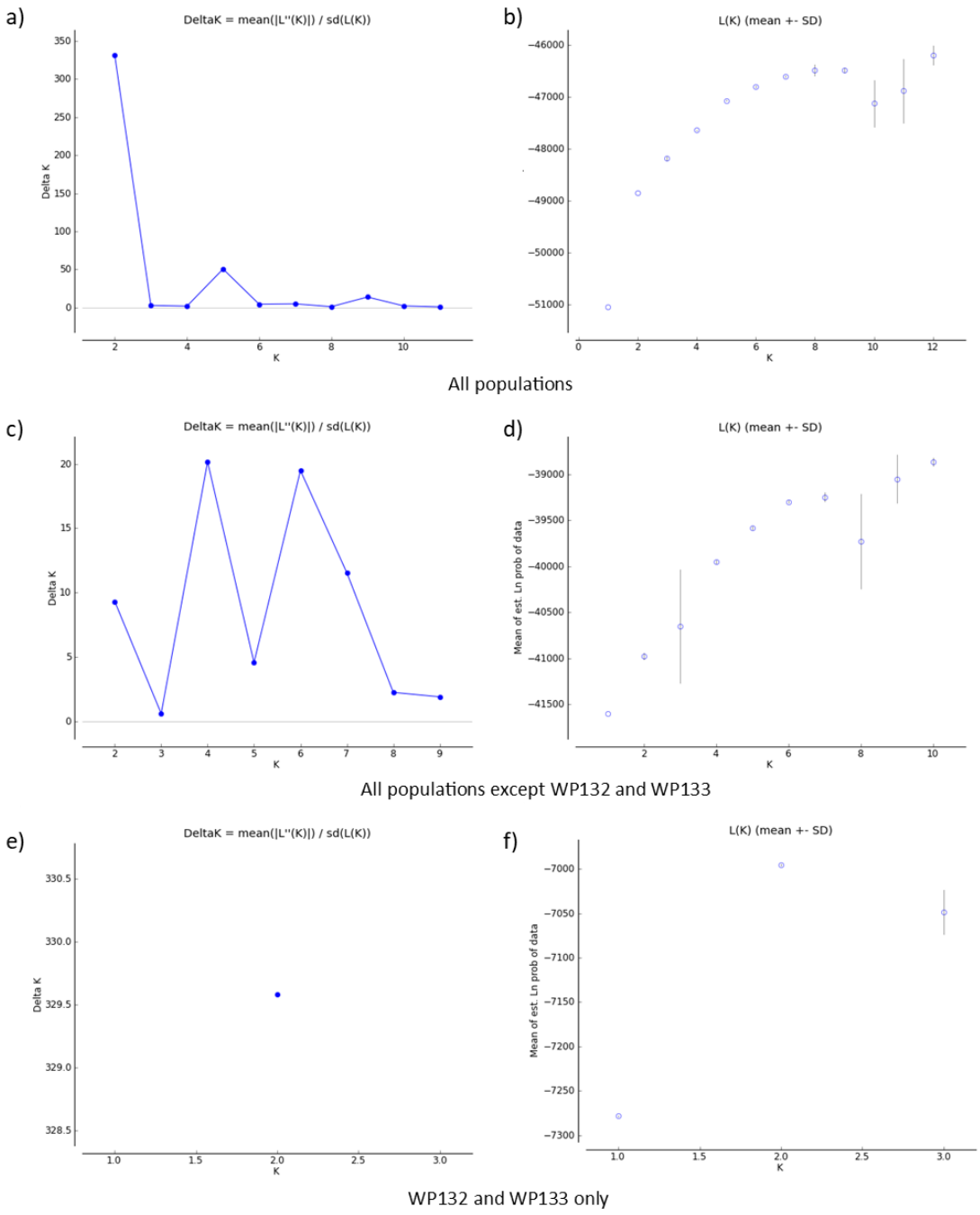
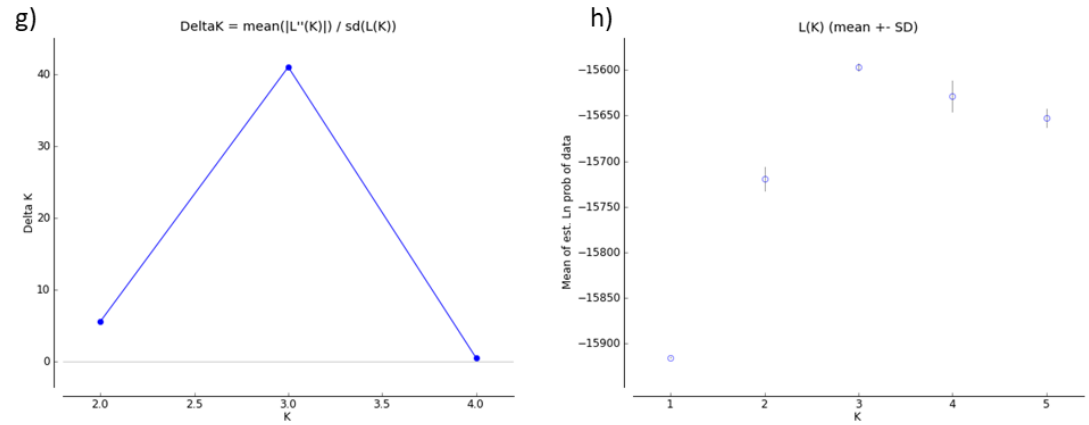
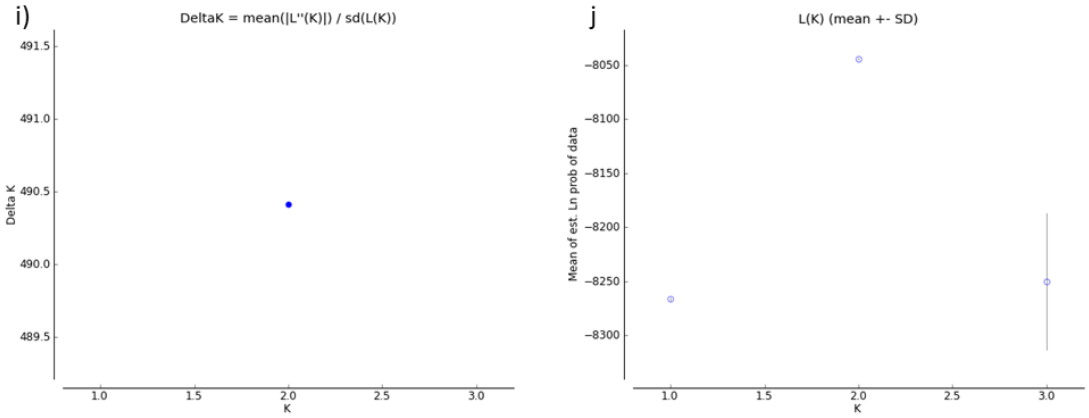


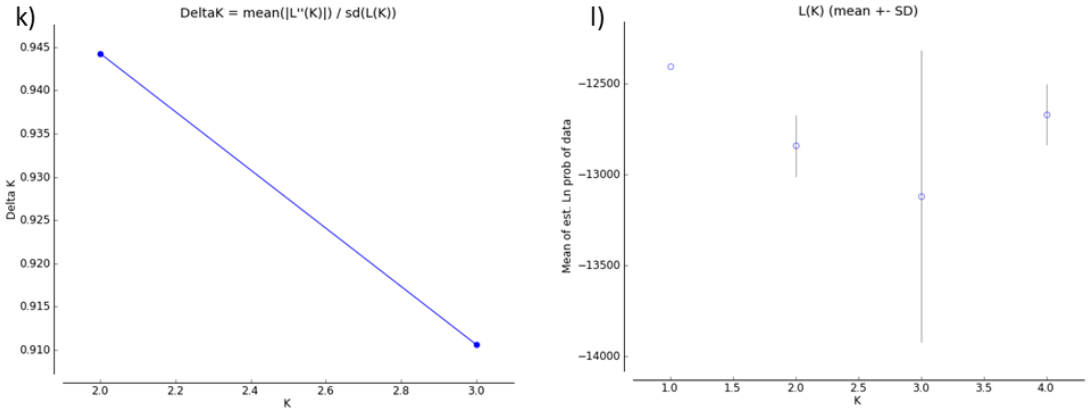
Fig.S2.3 Evanno and Ln Probability plots for all STRUCTURE analyses included in Fig.2.2. These include the Evanno and Ln Probability plot (respectively) for: all locations (a, b); all populations except the WP lakes (c, d); WP132 and WP133 only (e, f); the Nachvak sites (Schooner's Cove (SC), McCormick's River (MR), Ivatic Cove (IC), Palmer River (PR)) (g, h); Ramah Lake (RH) (i, j); Southwest Arm in 2007 and 2014 (SA07, SA14) and North Arm (NA) (k, l); SC, MR, IC only (m, n); SA07, SA14, NA with location priors (o, p); SC, MR, IC with location priors (q, r); SA07, SA14 with location priors (s, t). All plots were generated using STRUCTURE HARVESTER (Earl and vonHoldt 2012).



SC, MR, IC, PR



RH only



SA07, SA14, NA

Fig.S2.3 Continued.

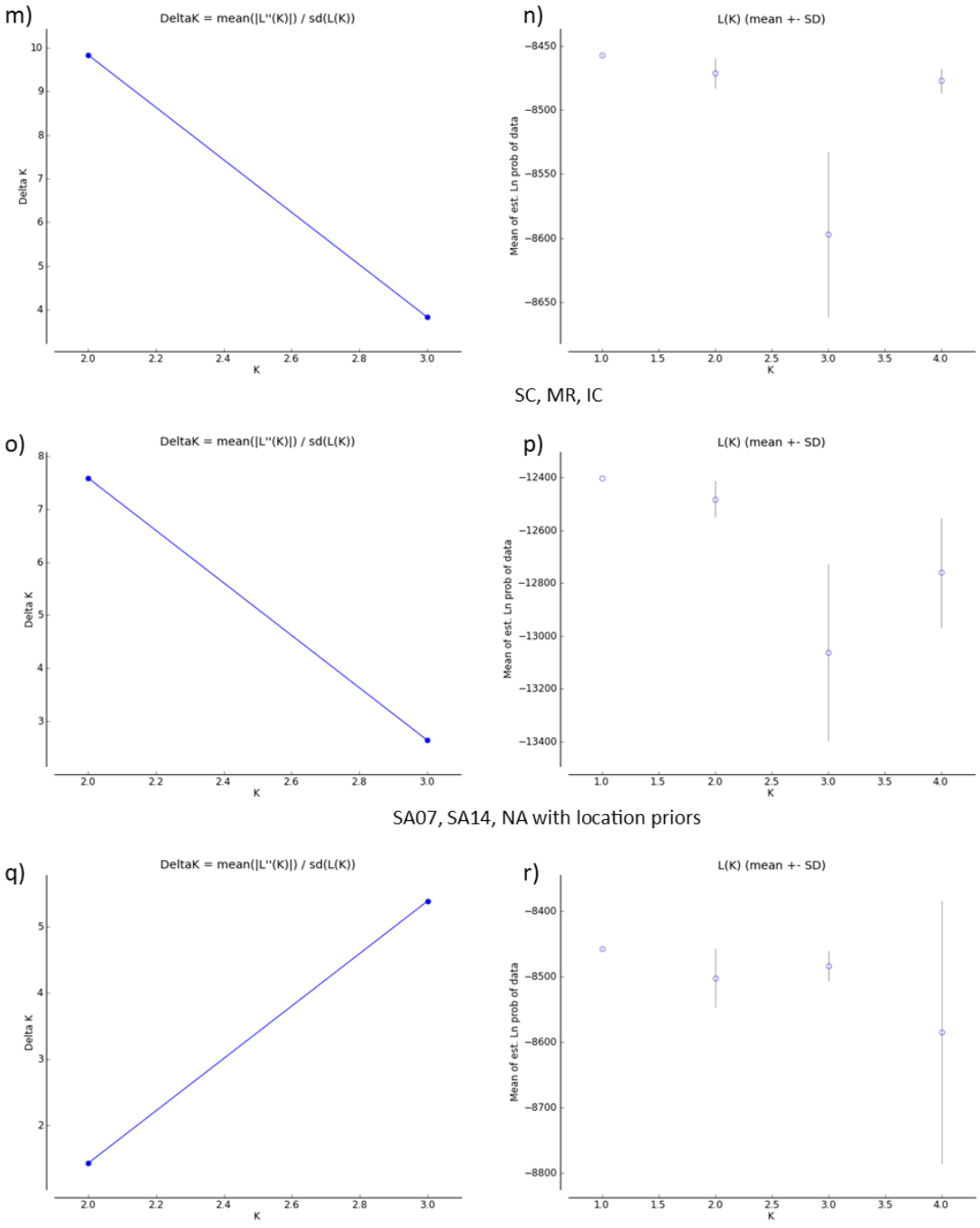


Fig.S2.3 Continued.

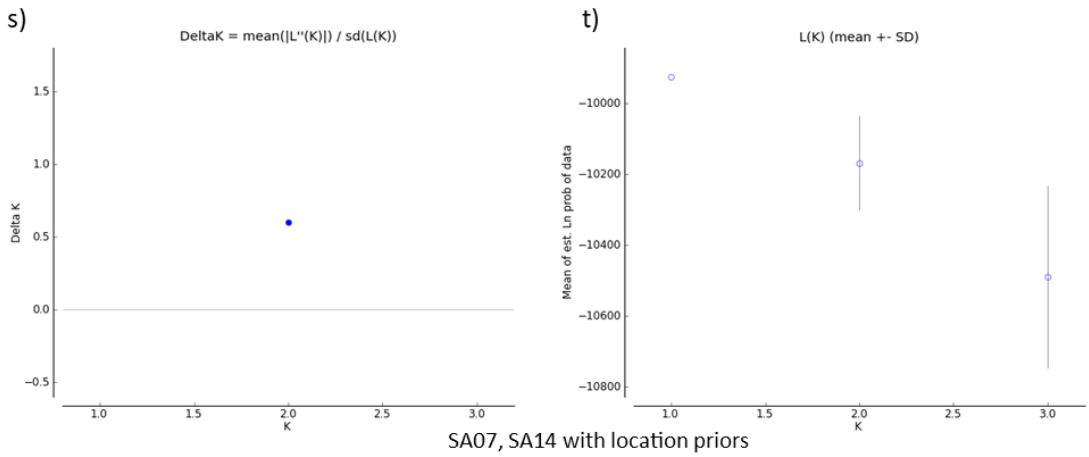


Fig.S2.3 Continued.

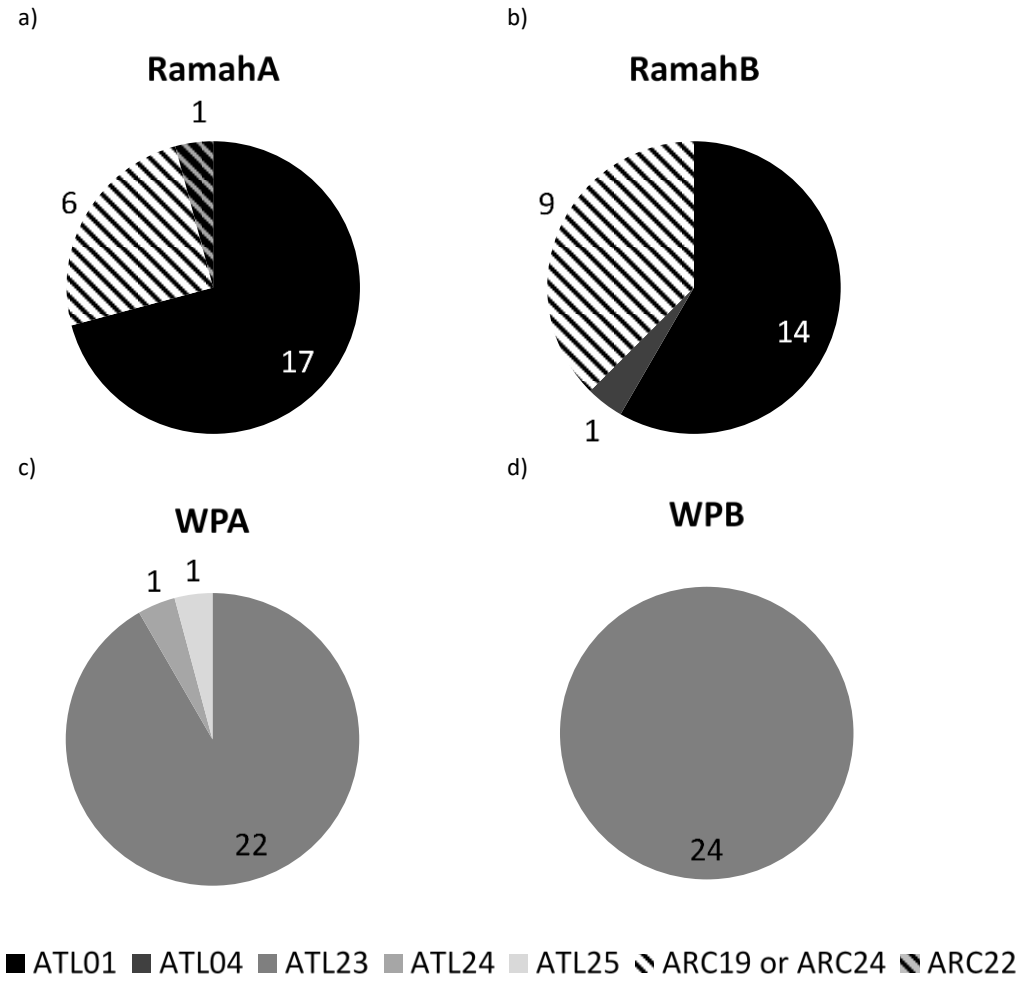


Fig.S2.4 Proportion of Arctic Charr (*Salvelinus alpinus*) mtDNA control region haplotypes detected in genetic subgroups a) RamahA, b) RamahB, c) WPA, d) WPB. The number of individuals associated with each haplotype slice is indicated.

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CHAPTER 3 - EXTENSIVE SECONDARY CONTACT AMONG THREE GLACIAL LINEAGES OF ARCTIC CHARR (*SALVELINUS ALPINUS*) IN LABRADOR AND NEWFOUNDLAND

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3.1 Abstract

Aim: The Pleistocene glaciation event prompted the allopatric divergence of multiple glacial lineages of Arctic Charr (*Salvelinus alpinus*), some of which have come into secondary contact upon their recolonization of the Holarctic. While three glacial lineages (Arctic, Atlantic, and Acadian) are known to have recolonized the western Atlantic, the degree of overlap of these three lineages is largely unknown. We sought to determine the distribution of these three glacial lineages in Labrador and Newfoundland at a fine spatial scale to assess their potential for introgression and their relative contribution to local fisheries.

Location: Labrador and Newfoundland, Canada

Methods: We sequenced a portion of the D-loop region in over 1000 Arctic Charr (*Salvelinus alpinus*) samples from 67 locations across Labrador and Newfoundland.

Results: Within Labrador, the Arctic and Atlantic lineages were widespread. Two locations (one landlocked and one with access to the sea) also contained individuals of the Acadian lineage, constituting the first record of this lineage in Labrador. Atlantic and Acadian lineage individuals were found in both eastern and western Newfoundland. Multiple sampling locations in Labrador and Newfoundland contained fish of two or more different glacial lineages, implying their introgression. Glacial lineage did not appear to dictate contemporary genetic divergence between the pale and dark morph of charr present in Gander Lake, Newfoundland. Both were predominately of the Atlantic lineage, suggesting the potential for their divergence in sympatry.

Main Conclusions: Our study reveals Labrador and Newfoundland to be a unique junction of three glacial lineages which have likely hybridized extensively in this region.

3.2 Introduction

Glaciation events are a significant driver of evolution, physically isolating species into separate glacial refugia which can undergo allopatric divergence for thousands of years (Hewitt 2000, 2004; Fraser et al. 2012). During allopatry, populations may experience differential selection and drift resulting in the formation of genetically distinguishable glacial lineages (Hewitt 2003; Ruzzante et al. 2008; Moore et al. 2015). Retreating glaciers allowed access to new environments, sometimes facilitating secondary contact (Hewitt 2000; Soltis et al. 2006; Swenson and Howard 2005). Upon secondary contact, glacial lineages may demonstrate: 1) extensive gene flow, leading to complete genomic introgression; 2) complete reproductive isolation and an absence of gene flow; 3) some intermediate level of gene flow (Hewitt 1988; Noor 1999; Schluter 2001). The degree of hybridization is likely to depend on the accumulated genetic divergence among lineages and on the adaptive quality of each gene (Hewitt 1988). The amount of genetic divergence accumulated between glacial lineages and the degree of erosion of this divergence in secondary contact zones can significantly influence the contemporary genetic structure of a species (Bernatchez and Wilson 1998; Hewitt 2000, 2004). These areas of secondary contact and hybridization therefore not only inform conservation management but also offer natural experiments for the study of the factors driving speciation (Hewitt 1988).

Arctic Charr (*Salvelinus alpinus*) is one species demonstrating multiple secondary contact zones between glacial lineages which arose from allopatry during the Pleistocene (Brunner et al. 2001; Moore et al. 2015). Five glacial lineages of Arctic Charr have been described based on mtDNA: Arctic, Atlantic, Acadian, Beringian, Siberian (Brunner et al., 2001; Moore et al., 2015). Evidence for secondary contact has been observed between the Beringian and Arctic lineages in Russia and western North America (Brunner et al. 2001; Moore et al. 2015; Esin et al. 2017; Oleinik et al. 2017) and between the Arctic and Atlantic lineages in Nunavut and Labrador, Canada and between the Atlantic and Acadian lineages in Newfoundland, Canada (Wilson et al. 1996; Brunner et al. 2001; Moore et al. 2015; Salisbury et al. 2018). However, our knowledge of these secondary contacts is at a coarse spatial scale, particularly in Atlantic Canada (Brunner et al. 2001; Moore et al. 2015).

The Laurentide Ice Sheet covered this region during the Pleistocene (Bryson et al. 1969). It retreated fully from Newfoundland between 13000 and 9000 years BP (Bryson et al. 1969; Dyke 2004; Shaw et al. 2006) and from Labrador between 9000 – 7500 years BP (Bryson et al. 1969; Jansson 2003; Occhietti et al. 2011). The vast quantities of fresh water draining from the retreating glaciers into the Atlantic Ocean allowed anadromous Arctic Charr to extensively colonize Labrador and Newfoundland (Power 2002b). Some of the lakes colonized by anadromous charr in Labrador subsequently lost their access to the sea resulting in contemporarily landlocked charr populations (Scott and Crossman 1998). Other anadromous charr populations (particularly in Newfoundland) lost their anadromous lifestyle and remain lacustrine residents year-round (Scott and Crossman 1998).

The glacial lineages present in anadromous versus landlocked populations remains largely unknown in this region. Landlocked and anadromous populations might have been founded by different lineages, for example, if one was better adapted to a particular environment or life history. Alternatively, landlocked populations could have been founded only by lineages that were present before access to these lakes was lost. Investigation of which lineages are present in these two types of populations may therefore give an indication of the timing of colonization by different glacial lineages (Moore et al. 2015).

Within-lake genetic structure, previously found in Labrador and Newfoundland charr populations, may also be influenced by glacial lineage. Glacial lineage has been suggested as the origin of the substantial genetic divergence observed between a pale and a dark morph documented for Gander Lake in Newfoundland (Gomez-Uchida et al. 2008). Salisbury et al. (2018) alternatively found that the genetic structure in two landlocked lakes and one sea-accessible lake in Labrador were unrelated to glacial lineage.

Anadromous Arctic Charr populations are economically significant and form the basis of a commercial, recreational and subsistence fishery in Labrador (DFO 2001; Dempson et al. 2008). Historic allopatry may be an important underlying influence on the genetic structure of the populations contributing to these fisheries if charr of different glacial lineages contribute to the fishery but remain reproductively isolated. While it is

currently unknown which glacial lineages contribute to the Labrador fishery this knowledge is potentially critical for its management.

Here we investigate the consequences of secondary contact of the Arctic, Atlantic and Acadian glacial lineages across Labrador and Newfoundland at a fine spatial scale. We predicted that the Arctic lineage would be more prevalent in northern populations than the Atlantic lineage based on the hypothesis that Labrador was colonized from the north by the Arctic lineage and from the south by the Atlantic lineage. Hybridization among lineages was expected to be prevalent and evidenced by multiple lineages co-existing in single populations. In Labrador, we anticipated that lineages which colonized more recently would be present only in the sea-accessible but not the landlocked populations. Finally, we hypothesized that the large divergence between the pale and dark morphs within Gander lake was due to their founding by different glacial lineages. To test these hypotheses we employed mtDNA to identify the glacial lineage of hundreds of fish across Labrador and Newfoundland.

3.3 Methods

3.3.1 Sampling

Tissue samples (N = 1329) were collected between 2000 and 2015 from Labrador and Newfoundland. Landlocked and sea-accessible Labrador locations were distributed among 10 drainages (fjords or bays). The samples from three sites in Labrador (Ramah (R01), WP132 (S03), WP133 (S04) were used previously in Salisbury et al. (2018). Collections from western Newfoundland originate from five landlocked lakes in the Upper Humber River (see Gomez-Uchida et al. 2009; Gomez-Uchida et al. 2013). Collections from eastern Newfoundland originate from two locations containing only freshwater residents: Gander lake (including samples of the pale and dark morphs described for this lake (Gomez-Uchida et al. 2008)), and Wing Pond.

Samples from Labrador were collected using electrofishing in the rivers (sea-accessible sites) and variably-sized standardized nylon monofilament gillnets (1.27 cm to 8.89 cm diagonal) at the landlocked and sea-accessible lake sites. Samples were collected from anadromous charr populations in the Okak and Voisey regions as well as from the Fraser River, Anaktalik River, and Tikkoatokak River. These populations contribute to

the three stock complexes of the commercial Labrador charr fishery (Okak, Voisey, Nain) (DFO 2001). Gander Lake was sampled using Lundgren multimesh gillnets (Hammar and Filipsson 1985) (bar length from 0.625 cm to 7.5 cm) (see Gomez-Uchida et al. 2008, for more details). The Upper Humber River was sampled using fyke nets and electrofishing (see Gomez-Uchida et al. 2009, for more details). Wing Pond was sampled with gillnets. Fish were weighed, measured for fork length (FL) in mm, and assessed for sex and maturity. Tissue samples (fin or gill) were obtained and immediately stored in 95% ethanol; alternatively, some fin clip samples were stored dry. All samples were collected in collaboration with the Department of Environment and Conservation for Labrador and Newfoundland and/or Parks Canada and in accordance with Dalhousie University's Animal Ethics Guidelines.

3.3.2 DNA Extraction, Amplification and Genotyping

Tissue samples were digested at 55ºC for approximately eight hours using Proteinase K (Bio Basic Inc., Markham, ON, Canada). DNA was then extracted using a Multiprobe II plus liquid handling system (Perkin Elmer, Waltham, MA, USA) using a glassmilk protocol modified from Elphinstone et al. (2003).

The left domain region of the mitochondrial control region was amplified and sequenced following Moore et al. (2015). In brief, the primers *Tpro2* (Brunner et al. 2001) and *SalpcrR* (Power et al. 2009) were used to amplify the entire control region using the thermocycler program and PCR outlined in (Brown Gladden et al. 1995). A shorter fragment was amplified using *Char3* instead of *Tpro2* for a minority of samples which had poor quality as determined from visual inspection of a 1% agarose gel. For all samples, a total of ~500 bp of the left domain was sequenced using *Char3* (Power et al., 2009) at MacrogenUSA (Rockville, MD). Each unique haplotype detected was validated by resequencing a representative sample for each haplotype using *Tpro2*.

3.3.3 Analyses

Our sequences were trimmed, validated, and aligned using GENEIOUS (10.0.9, Auckland, NZ, www.geneious.com). Using default alignment parameters our sequences were aligned along with a reference haplotype set (including control region haplotypes

verified by Moore et al. (2015) and Salisbury et al. (2018)), and the control region sequences for three other salmonid species present in the study region Brook Trout (*Salvelinus fontinalis*), Lake Trout (*Salvelinus namaycush*), and Atlantic Salmon (*Salmo salar*) (for accession numbers see Table S3.1, Supporting Information). Sequences verified as Arctic Charr were ascribed to the reference haplotype(s) for which they had 0 basepair differences. Non-charr sequences were ascribed to the Brook Trout, Lake Trout or Atlantic Salmon haplotype to which they had the minimum number of basepair differences.

A representative forward sequence for each unique haplotype (i.e., those sequences which contained one or more basepair differences from those haplotypes verified by Moore et al. (2015)) was aligned with its reverse complement (sequenced with *Tpro2*) using a pairwise Geneious alignment and default parameters to create a consensus sequence. The consensus sequences for these unique haplotypes were then aligned with the reference haplotype set using a Geneious alignment. A gap penalty of 7 was used and all other parameters were kept at default values. A maximum-likelihood tree was constructed based on this alignment using the PhyML (Guindon and Gascuel 2003) plugin in GENEIOUS to compare the phylogenetic relationships among these unique consensus sequences with those haplotypes verified by Moore et al. (2015) and those of an outgroup species (Brook Trout). The Nearest Neighbour Interchange topology search algorithm and the HKY85+I+G model was used to calculate 1000 bootstraps for each node following Moore et al. (2015).

A haplotype map based on all unique haplotypes found in this study along with all haplotypes verified by Moore et al. (2015) was created using PopArt version 1.7 (Leigh and Bryant 2015). Haplotypes were trimmed to 501 bp, the length for which all haplotypes had no missing basepairs, since PopArt masks missing basepairs. This meant that haplotype ATL04 and a unique haplotype ATL31 were indistinguishable in this analysis since the SNP differentiating these haplotypes lies outside of this 501 bp region. The haplotype map was created using a Median-Joining network (Bandelt et al. 1999) with an Epsilon value of 0.

A spatial analysis of molecular variance (SAMOVA 2.0) (Dupanloup et al. 2002) was employed to detect groups of sampling locations whose F_{CT} were maximally

differentiated based on mtDNA sequences. All sequences were aligned using Geneious alignment and default parameters and trimmed to 482 bp to include all relevant SNPs differentiating haplotypes. Sampling locations with fewer than 10 sequences were excluded from the analysis to minimize the probability of biased groupings due to small sampling size. F_{CT} values were estimated using a simulated annealing optimization process for K = 2 – 10 groups for all sampling locations and for only the Labrador sampling locations and for K = 2 - 4 groups for only the Newfoundland sampling locations. For each K-value, molecular distance was calculated using Tamura and Nei distance between all sampling locations and between only those sampling locations connected using a Delaunay network (Delaunay 1934) based on the latitude and longitude of each sampling location. The use of a Delaunay network limits groupings to geographically proximate sampling locations. Simulations were run for 10000 steps from 100 initial configurations using a missing data value of 1 (such that the entire 482 bp was included in the analysis).

Linear regressions between latitude and the number of lineages present in each location as well as binomial logistic regressions of latitude on the presence or absence (coded as 1 and 0, respectively) of each of the relevant glacial lineages were conducted using R (R Core Team 2013) for all locations, only Labrador locations, and only Newfoundland locations.

3.4 Results

3.4.1 Species Distribution

Samples from 59 locations in Labrador (of which 43 are sea-accessible and 16 are landlocked (Anderson, 1985)) and eight locations in Newfoundland (all containing lacustrine residents) for a total of 67 locations overall were successfully sequenced (Table 3.1). Five locations in Labrador were excluded from analyses due to poor sequence quality (N = 109 individuals). A further 20 individuals from across the remaining 67 locations were excluded from analyses due to poor sequence quality. A total of N = 1296 individuals were successfully sequenced across all locations in Labrador and Newfoundland (Table 3.1). Of these, 1133 had haplotypes consistent with the Arctic Charr species. The remaining 163 individuals were identified as Brook Trout, Lake

Trout, or Atlantic Salmon. All locations contained at least one Arctic Charr haplotype except G06 which only contained Atlantic Salmon. In the remaining locations we sampled between 1 - 48 Arctic Charr (median = 18.5), which made up between 2% - 100% of the haplotypes in each sample.

3.4.2 Glacial lineage distribution

The Arctic and Atlantic glacial lineages were ubiquitous across Labrador and both lineages were present in all 10 drainages (Fig.3.1a). The Arctic and Atlantic lineages were detected in 49 and 48 locations, respectively, and they co-occurred in 39 locations. The Acadian lineage was detected in only two sampling locations in Labrador. In one landlocked location (A02, Fig.3.1a), all charr samples were of the Acadian lineage. The second location was sea-accessible (W03, Fig.3.1a) and it contained one individual of the Acadian lineage among one Arctic lineage and six Atlantic lineage individuals.

Only the Atlantic and Acadian lineages were detected in Newfoundland (Fig.3.1b,c). The Atlantic lineage was detected in 3/5 locations in western Newfoundland and both locations in eastern Newfoundland. The Acadian lineage was detected in all five locations of western Newfoundland but only a single Acadian lineage individual was detected in a pale morph charr from Gander Lake in eastern Newfoundland.

The overlap in the distributions of these three lineages in Labrador is suggested by a lack of correlation between latitude and the number of lineages present in each sampling location across all locations ($R^2_{(64)}$= 0.036, $p \geq 0.12$), in only Labrador sites ($R^2_{(57)}$= 0.015, $p \geq 0.36$), and in only Newfoundland sites ($R^2_{(5)}$= 0.29, $p \geq 0.21$). Binomial logistic regressions of latitude on the presence or absence (coded as 1 and 0, respectively) of the Arctic and Atlantic lineages in each Labrador sampling location were not significant ($p \geq 0.699$, $p \geq 0.145$, respectively). Similarly, there was no significant relationship between latitude and the presence of the Atlantic and Acadian lineages in Newfoundland sites ($p \geq 0.38$, $p \geq 0.350$, respectively). Across all sampling locations, the presence of the Atlantic lineage was unrelated with latitude ($p \geq 0.435$). However, across Labrador and Newfoundland the probability of Arctic lineage presence increased with latitude ($p \leq 6.46 \times 10^{-3}$). Similarly, the presence of the Acadian lineage was inversely related to latitude ($p \leq 1.08 \times 10^{-4}$).

3.4.3 Haplotype Distribution

The most common haplotype within a lineage coincided with the most common haplotypes reported in Moore et al. (2015) (haplotypes at each location: see Table S3.2). A total of 86% of Atlantic lineage individuals exhibited haplotype ATL01, while 78% of Acadian lineage individuals exhibited haplotype ACD9. All Labrador samples of the Acadian lineage had this haplotype. Lastly, over 99% of Arctic lineage individuals exhibited haplotypes ARC19 or ARC24. These two haplotypes were distinguished by a single SNP outside of the region sequenced using the *Char3* primer. However, the reverse complement of 29 samples from 28 locations and nine drainages with either the ARC19 or ARC24 haplotype was sequenced using *Tpro2* and all were found to have the haplotype ARC19. Therefore, unambiguously ARC19 sequences were grouped with sequences that could be either ARC19 or ARC24 when counting the number of haplotypes present in a given site. The ARC19, ATL01, and ACD9 haplotypes were found across the modern distributions of the Arctic, Atlantic, and Acadian lineages respectively by Moore et al. (2015).

Other detected haplotypes which had been previously described by Moore et al. (2015) and Salisbury et al. (2018) include ACD11, ARC20, ARC22, ATL19, ATL23, ATL24 and ATL25. A single sample had the ATL19 haplotype, a dark morph charr from Gander. This was also the only Atlantic haplotype other than ATL01 detected in Newfoundland. The ATL23, ATL24 and ATL25 haplotypes were only observed in S03 and S04 as described in Salisbury et al. (2018) except for one individual with ATL23 found in S02. This individual may have been washed downstream from the immediately upstream landlocked S03 and S04. This is supported by its identification as a putative migrant from S03 based on GENECLASS2 (Piry et al. 2004) results as reported in Salisbury et al. (2018).

Five samples from three landlocked sites in the Voisey drainage had shortened sequences that prevented their differentiation between ATL01 and ATL04. Since these sites also contained individuals unambiguously identified as ATL01, these shortened sequences were considered to be ATL01 when counting the number of haplotypes present in these lakes. The ATL04 haplotype was also found in 12 sea-accessible sampling locations across seven drainages in Labrador. The reverse complement of nine of these

samples from 6 drainages was sequenced using *Tpro2* and all were found to contain a consistent SNP in the consensus sequence, differentiating this haplotype from ATL04. One of these samples was from R01, previously mistakenly identified as ATL04 in Salisbury et al. (2018). Given the consistency of this SNP across samples from multiple drainages, sampling locations, and studies, we denoted this as a new haplotype ATL31. We considered all ATL04 haplotypes and verified ATL31 haplotypes to be a single haplotype when counting the number of haplotypes present in the 12 sea-accessible sampling locations where these haplotypes were observed.

Including ATL31 there were eight haplotypes not previously identified by Moore et al. (2015) or Salisbury et al. (2018) (Accession Numbers: MK208868 - MK208871, MK208875 - MK208878) (Fig.3.2). All new haplotypes were one base pair different from another haplotype verified by Moore et al. (2015) within their assigned lineage (Fig.3.3). These include three Acadian haplotypes (ACD12, ACD13, ACD14) only observed in western Newfoundland. Four new Atlantic haplotypes were identified (ATL26, ATL28, ATL29, ATL31). ATL26 was found in only one individual in A01. ATL28 was found in three individuals, one in F01, one in T01, and one in T02. ATL29 was found in one individual in N01. Only one new Arctic haplotype, ARC35, was observed in a single individual in T01. All new haplotypes except ATL31 were found to be at least 1 base pair different from the top hit when compared with the NCBI nr/nt database using the Megablast algorithm. ATL31 was found to have 100% identity with an Arctic Charr sample (Accession Number: KY122252) collected from Lake Sitasjaure, Sweden (Oleinik et al. 2017).

3.4.4 Landlocked versus Sea-accessible Sampling Locations

The average number of lineages observed in anadromous sites was higher than in landlocked sites (average of 1.8 lineages for anadromous sites versus 1.3 lineages for landlocked sites, $T_{(42)} = 3.78$, $p \leq 0.001$). Similarly, the average number of haplotypes observed in anadromous sites was higher than in landlocked sites (average of 2.3 haplotypes for anadromous sites versus 1.8 haplotypes for landlocked sites, $T_{(45)} = 1.96$, $p \leq 0.056$). (Note: the Gander lake morphs (I01/I02) and Wing Pond were grouped with the landlocked lakes despite both lakes having access to the sea because their charr are

lacustrine residents.) This effect was even more extreme when considering only Labrador sites where the corresponding average numbers were 2.3 and 1.5 haplotypes in anadromous and landlocked sites, respectively ($T_{(40)} = 3.56$, $p \leq 0.001$). Anadromous sites in Labrador also had an average of 1.8 lineages per site, significantly more than the 1.3 lineages observed in landlocked sites ($T_{(26)} = 3.63$, $p \leq 0.0012$).

3.4.5 SAMOVA

SAMOVA results were similar across all samples and when considering Labrador and Newfoundland sampling locations separately. Results were also similar with and without the use of a Delaunay network to take into account geographic proximity of locations. For brevity, we report only the SAMOVA results when considering all sampling locations and a Delaunay network (for results of all other SAMOVA analyses see Fig.S3.1, S3.2).

When considering all sampling locations, F_{CT} was maximized for K = 6 (Fig.3.4). However, the difference in F_{CT} between K = 6 and K = 5 was small (i.e., 0.07) and a plot of F_{CT} versus K revealed that F_{CT} leveled off at K = 5 (Fig.S3.1a). Given this small difference in F_{CT} we report the more parsimonious results of K = 5. The first group contained 26 populations across Labrador with approximately equal proportions of Arctic and Atlantic lineage individuals. The second group contained only Arctic lineage individuals and comprised 4 locations in Labrador, three in the Okak and one in the Saglek drainage. The third group comprised only one Labrador site, A02, which contained only Acadian lineage individuals. The fourth group contained 16 populations, 14 in Labrador and two in eastern Newfoundland. This group comprised largely Atlantic lineage individuals. The fifth group contained the three landlocked lakes in western Newfoundland.

3.5 Discussion

3.5.1 Extent of Secondary Contact

Our results indicate an extensive overlap in the contemporary ranges of the Arctic, Atlantic and Acadian lineages in Labrador and Newfoundland. A SAMOVA detected groupings from geographically separate locations which indicates the

widespread distribution of these three lineages. The two detected groupings with the highest number of locations (orange and purple groups in Fig.3.4) spanned the entirety of the latitudinal range sampled in Labrador. The orange group (Fig.3.4), which included locations with predominately Atlantic lineage fish, also included the eastern Newfoundland locations, reflecting the extensive colonization of the Atlantic lineage throughout Labrador and Newfoundland.

The Arctic and Atlantic lineage haplotypes were observed across the full latitudinal range studied in Labrador, suggesting that secondary contact has occurred at multiple times and locations among these lineages within this region. Contrary to our hypothesis, there was no association between latitude and presence of the Arctic or Atlantic lineage in Labrador, indicating that the region in which secondary contact has occurred between these lineages is at least as extensive as our study area. Our results represent the furthest north an Atlantic haplotype has been observed in Labrador (N01, ~59° N). This observation is consistent with evidence for an incursion of Atlantic lineage nuclear DNA, but not mtDNA, in Nunavut (Moore et al. 2015). Our results also include the furthest south an Arctic lineage haplotype has been observed in the Atlantic (W06, ~55° N). It is possible that the Arctic lineage may have colonized even further south into Labrador than the range considered here. The extent of secondary contact and introgression among lineages may also be underestimated since mtDNA haplotypes reflect only maternal inheritance.

While the majority of locations in Labrador contained both the Arctic and Atlantic lineages, four populations in Labrador contained exclusively Arctic lineage samples. This group of four lakes was detected as significant by SAMOVA (blue locations in Fig.3.4). The absence of Atlantic lineage haplotypes (which are present in nearby populations) from these locations may have been lost through drift. Alternatively, colonization by the Atlantic lineage may have been prevented by their maladaptation to these sites ("isolation-by-adaptation") or their exclusion by the previously established Arctic lineage ("isolation-by-colonization") (Waters 2011; Orsini et al. 2013; Waters et al. 2013).

Unlike the Atlantic lineage, the Arctic lineage does not appear to have invaded Newfoundland. The absence of the Arctic lineage from Newfoundland may be due to our low sample sizes and the fewer number of locations sampled. However, our study

confirmed the previous observations of the Atlantic and Acadian lineage in eastern Newfoundland (Brunner et al. 2001; Moore et al. 2015). We also demonstrated that the contemporary range of both the Atlantic and Acadian lineages extends to western Newfoundland.

Our extension of the Acadian lineage's contemporary presence into Labrador counters previous suggestions of its relatively conserved range from its putative refugium near the northeastern United States (e.g., Brunner et al. 2001; Esin and Markevich 2018). This brings the scale of the contemporary range of the Acadian lineage in line with those observed in other charr lineages.

3.5.2 Evidence for Introgression

Our results here suggest extensive secondary contact but also the introgression of the Arctic, Atlantic and Acadian lineages in Labrador and Newfoundland. Many sampled locations contained at least two glacial lineages suggesting the potential for hybridization among lineages. Furthermore, we found six sea-accessible locations in Nachvak and Saglek fjords (N01-N04, S01-S02) contained both Arctic and Atlantic lineage individuals based on mtDNA, yet no genetic structuring was found within each of these same locations based on 11 microsatellite markers in Salisbury et al. (2018). This suggests that these lineages have fully introgressed.

Hybridization between these lineages may seem surprising given that Arctic lineage is thought to have split off from all other lineages between 716000 and 1432000 years BP based on mtDNA (Moore et al. 2015). Alternatively, Esin and Markevich (2018) estimate the divergence of the Arctic lineage at 400000 – 700000 years BP during the Nebraskan-Kansan cooling. During this time the Canadian Arctic archipelago (the putative refugium for the Arctic lineage) was separated from a refugium in the Bering Sea (Esin and Markevich 2018). Many species have demonstrated reproductive isolation between different glacial lineages upon secondary contact within such a time scale (Bernatchez and Wilson 1998; Hewitt 2003). However, our results support previous research suggesting hybridization among Arctic Charr glacial lineages. Atlantic lineage nuclear DNA has been found in Nunavut populations of Arctic lineage individuals (Moore et al. 2015). A similar lack of a relationship between mtDNA and nuclear DNA

has also been observed in Three-spined Stickleback (*Gasterosteus aculeatus*) (Lescak et al. 2017). Many *Salvelinus* species are known to readily hybridize (Taylor 2004), and there is evidence for Arctic Charr having hybridized with Brook Trout in Quebec (Bernatchez et al. 1995; Glémet et al. 1998) and Labrador (Fraser River) (Hammar et al. 1991) and with Lake Trout in Nunavut (Wilson and Hebert 1993) and Quebec (Wilson and Bernatchez 1998). These hybridizations overcome a much older allopatric divergence than that among Arctic Charr glacial lineages. Hybridization between species does not necessarily mean intraspecific glacial lineages may hybridize. However, given the relatively short duration of allopatric divergence, the lack of reproductive isolation among glacial lineages is unsurprising.

Some of the Brook Trout and Lake Trout mtDNA haplotypes detected in our samples may therefore reflect hybridization or backcrosses between these species and Arctic Charr. This would require further validation using nuclear markers but was beyond the scope of this study. An open area for future investigation is the degree to which genes from Lake Trout and Brook Trout have introgressed into Arctic Charr genomes within this region.

3.5.3 Colonization History

We detected several rare haplotypes that were previously found in other populations within each lineage's respective range allowing for insight into the origins of the three glacial lineages in this region. The ARC20 and ARC22 haplotypes we detected in Labrador were previously observed in geographically distinct locations across the high Canadian Arctic (Moore et al. 2015). The Arctic lineage may have therefore colonized Labrador multiple times from geographically distant populations. The ATL19 haplotype we observed in a single dark charr morph in Gander Lake was previously observed in an unspecified morph in this lake as well as in a resident lacustrine population from Scotland (Moore et al. 2015). Lastly, the ATL31 haplotype we found in multiple anadromous populations was also found in a landlocked, Swedish population (Oleinik et al. 2017). The appearance of these Atlantic haplotypes on opposite sides of the Atlantic Ocean suggests extensive colonization throughout the Atlantic from the Atlantic refugium. While our study area demonstrates a high diversity of Atlantic lineage haplotypes, this

diversity is no doubt due to our intensive sampling. Whether the Atlantic refugium was located on the western or eastern side of the Atlantic therefore requires further investigation.

3.5.4 Landlocked vs. Sea-accessible locations

It was not possible to determine the order in which the glacial lineages colonized Labrador based on the lineages present in landlocked versus sea-accessible locations. All three lineages were present in both landlocked and sea-accessible locations in Labrador. Moore et al. (2015) suggested the Atlantic lineage had colonized the high Canadian Arctic after the Arctic lineage since some anadromous charr populations contained Atlantic lineage nuclear DNA but nearby landlocked charr populations demonstrated Arctic lineage nuclear DNA. Our results suggest that all three lineages may have colonized Labrador around the same time.

Though they did not share a common lineage, most landlocked populations contained a single lineage and low haplotypic diversity. This could be due to a founder-take-all scenario, where the lineage that first colonized a lake rapidly expanded to fill available habitat, preventing subsequent incursions from other lineages (Waters 2011; Orsini et al. 2013; Waters et al. 2013). Also, landlocked populations, are more isolated and tend to exhibit smaller effective sizes (see Salisbury et al. 2018) and thus experience more drift than anadromous populations potentially leading to a greater loss of mtDNA haplotypes.

Several landlocked lakes countered this trend of reduced diversity. Landlocked lakes within the Kogaluk River system (i.e., V10, V11, V15, V16) had Arctic and Atlantic lineage charr co-occurring. Access to this watershed may have been enhanced by significant run-off from the paleolake Naskaupi, which drained through the Kogaluk between 7500 and 6000 years BP (Barnett and Peterson 1964; Jansson and Kleman 2004). Alternatively, many lakes within the Kogaluk River drainage are connected via shallow streams which could facilitate the occasional migration between lakes as it has for Lake Trout (McCracken et al. 2013) and longnose suckers (*Catostomus catostomus*) (Salisbury et al. 2016) in this system. Migration may have countered genetic drift (Tallmon et al. 2004), maintaining both Arctic and Atlantic lineage haplotypes in these

lakes. High effective sizes (Gomez-Uchida et al. 2013) and high migration among lakes (Gomez-Uchida et al. 2009) may have similarly countered the effects of genetic drift in landlocked populations in western Newfoundland (G02-G04) which contained both Atlantic and Acadian lineages as well as high haplotypic diversity within the Acadian lineage.

3.5.5 Glacial lineage and contemporary morph divergence in Gander Lake

Previous work has suggested that the high degree of neutral genetic differences observed between pale and dark morph charr could be ascribed to differential glacial origins (Gomez-Uchida et al. 2008). Our results, indicating that most charr in Gander Lake were of the Atlantic lineage regardless of morph (aside from a single Acadian lineage pale morph char), reject this hypothesis. This suggests that the great morphological, ecological, and genetic differences between the pale and dark morph (O'Connell and Dempson 2002b; Power et al. 2005; Gomez-Uchida et al. 2008) may have arisen in sympatry in Gander Lake within the last ~ 10000 years since its deglaciation (Bryson et al. 1969; Dyke 2004; Shaw et al. 2006). This is consistent with the presumed sympatric divergence of other lacustrine Arctic Charr morphs (Magnusson and Ferguson 1987; Volpe and Ferguson 1996; Gíslason et al. 1999). The large genetic divergence among pale and dark morph charr in Gander suggests substantial genetic differences can accumulate between morphs within a short period of time, potentially fueled by divergent selection (Taylor 2004) and the relatively low effective population sizes of both pale and dark charr (Gomez-Uchida et al. 2008).

The occurrence of Atlantic and Acadian lineages in the pale morph suggests introgression of these lineages. Similar evidence for introgression among the Arctic and Atlantic lineages was found in R01 by Salisbury et al. (2018), where morphologically identified anadromous and resident charr were found to be genetically differentiated by STRUCTURE but each contained both Arctic and Atlantic lineage individuals. Populations of sympatric dwarf and normal whitefish (*Coregonus clupeaformis*) in Maine have also each demonstrated both of two mtDNA haplotype groups (indicative of two glacial lineages) (Bernatchez and Dodson 1990; Pigeon et al. 1997). These observations lead to the puzzling implication that glacial lineages have introgressed despite thousands

of years of allopatric divergence yet, in some cases, their descendants have become reproductively isolated (perhaps in sympatry) and subsequently significantly diverged in the (relatively) short time since deglaciation.

3.5.6 Management Implications and the Utility of Intensive mtDNA Sampling

The likely introgression among glacial lineages in Labrador has important implications for the charr fishery in Labrador. There was evidence of Arctic, Atlantic and even Acadian lineage fish in sea-accessible locations in the Notakwonan, Voisey, Anaktalik, Nain, and Okak drainages. These populations probably contribute to the commercial fishery stock complexes (DFO 2001; Dempson et al. 2008). The expected introgression between lineages suggests that there is likely no need to manage them separately; however, this should be further validated by investigating the relative lineage makeup of commercially caught charr.

Our results verify the utility of intensive mtDNA sampling across many populations, particularly within a secondary contact zone. This approach facilitated the detection of a number of new haplotypes for the Arctic, Atlantic and Acadian lineages (Fig.3.2, 3.3) as well as the detection for the first time, of the Acadian lineage within Labrador. Finally, our detection of non-Arctic Charr salmonid species highlights the morphological ambiguity of salmonids, particularly as juveniles. All of the samples identified genetically as a species other than Arctic Charr had a median length of 40 mm (data not shown). Since species misidentification can have repercussions for the interpretation of genetic data we therefore caution against the exclusive use of morphology in juveniles in regions where other salmonids coexist with Arctic Charr. The mtDNA-based technique as used here is useful for minimizing the possibility of species misidentification in regions where other salmonid species overlap with Arctic Charr.

In conclusion, our results clearly demonstrate the widespread secondary contact of the Arctic, Atlantic, and Acadian glacial lineages of Arctic Charr throughout Labrador and Newfoundland, Canada. These three glacial lineages have likely introgressed extensively in this region. The genetic divergence in morph pairs in Ramah and Gander lakes do not appear to be linked to glacial lineages. We demonstrate that Arctic Charr are

an ideal model species for future investigation of secondary contact zones and the influence of historical allopatry on contemporary genetic structure and niche divergence.

3.6 Data Accessibility Statement

Newly identified Arctic Charr mtDNA D-loop haplotypes were submitted for archival with GenBank (Accession Numbers: (Accession Numbers: MK208868 - MK208871, MK208875 - MK208878)

3.7 Author Contributions

DER., SJS designed the study; all authors collected samples; GRM., SJS completed lab work; SJS analysed data and led the writing.

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3.9 Tables

Table 3.1 Number of Arctic Charr (*Salvelinus alpinus*) samples, glacial lineages, and haplotypes as well as number of Brook Trout (*Salvelinus fontinalis*), Lake Trout (*Salvelinus namaycush*), and Atlantic Salmon (*Salmo salar*) samples verified by mtDNA sequencing at sampling locations across Labrador and Newfoundland. Accessibility of locations (A for sea-accessible, L for landlocked).

Site	Drainage	Watershed	Latitude, Longitude	Access	Number of *S. fontinalis*	Number of *S. namaycush*	Number of *S. Salar*	Number of *S. alpinus*	Number of *S. alpinus* Lineages	Number of *S. alpinus* Haplotypes
N01	Nachvak	Schooner	59°05'47.50, -63°30'33.58	A				15	2	3
N02	Nachvak	Palmer River	58°56'59.60, -63°52'55.35	A				24	2	2
N03	Nachvak	McCormick's River	59°01'00.94, -63°44'39.15	A				24	2	3
N04	Nachvak	McCormick's River	59°00'28.61, -63°44'16.21	A				19	2	2
R01	Ramah	Stecker River	58°50'28.96, -63°28'38.66	A				48	2	4
S01	Saglek	North Arm Brook	58°32'53.92, -63°27'38.09	A				25	2	2
S02	Saglek	Southwest Arm Brook	58°29'07.27, -63°27'47.04	A				24	2	4
S03	Saglek	Southwest Arm Brook	58°16'48.58, -63°58'09.47	L				24	1	1
S04	Saglek	Southwest Arm Brook	58°16'18.02, -64°01'52.90	L				24	1	3
S05	Saglek	Pangertok Inlet River	58°19'46.64, -63°11'05.05	A				14	2	3
S06	Saglek	Kiyuktok Brook	58°26'55.46, -62°48'36.36	A				23	1	1
H02	Hebron	Ikarut River	58°09'17.07, -63°06'10.56	A				23	2	3
H03	Hebron	Ikarut River	58°10'25.72, -63°17'37.74	A	8			16	2	3
H04	Hebron	Ikarut River	58°08'46.00, -63°35'28.77	L				24	1	1
H05	Hebron	Hebron	58°03'42.64, -63°12'54.67	A				4	2	2
H07	Hebron	River 105 (Unnamed)	58°05'10.83, -63°43'50.18	A				24	2	2
H09	Hebron	River 104 (Unnamed)	57°56'11.77, -63°28'31.80	A				24	2	2
H10	Hebron	River 104 (Unnamed)	57°51'57.96, -63°32'22.08	A	2			22	2	2
H11	Hebron	River 104 (Unnamed)	57°50'20.23, -63°32'20.79	A				21	2	3
H12	Hebron	River 104 (Unnamed)	57°46'29.73, -63°36'50.69	A				3	2	2
H13	Hebron	Unnamed River	57°58'16.60, -63°12'56.64	A				24	2	2
H14	Hebron	River 103 (Unnamed)	58°02'23.19, -63°01'55.97	A				23	2	3
H15	Hebron	River 103 (Unnamed)	58°00'37.93, -63°02'25.85	A	3			20	2	2
H16	Hebron	River 103 (Unnamed)	57°44'37.87, -63°21'10.96	A				18	2	2
K01	Okak	Siugak Brook	57°37'02.94, -62°10'46.77	A	11		6	7	2	2
K02	Okak	Siugak Brook	57°36'07.39, -62°25'25.77	A	26			6	1	1
K03	Okak	Siugak Brook	57°43'35.33, -62°28'24.10	A				24	1	1
K04	Okak	Siugak Brook	57°39'41.79, -62°57'16.01	L				21	1	2

Table 3.1 Continued.

Site	Drainage	Watershed	Latitude, Longitude	Access	Number of *S. fontinalis*	Number of *S. namaycush*	Number of *S. Salar*	Number of *S. alpinus*	Number of *S. alpinus* Lineages	Number of *S. alpinus* Haplotypes
K05	Okak	North River	57°30'05.72, -62°44'35.43	A				24	2	3
K06	Okak	North River	57°38'20.95, -63°13'58.52	L				24	1	1
T01	Tikkoatokak	Kingurutik River	56°52'48.33, -62°37'19.58	A				24	2	5
T02	Tikkoatokak	Kingurutik River	57°08'55.83, -62°52'41.37	A				26	1	2
T03	Tikkoatokak	Kingurutik River	57°17'08.88, -63°42'48.22	A		1		7	1	1
T04	Tikkoatokak	Kamanatsuk Brook	56°44'19.87, -62°33'48.41	A	3			21	2	2
T05	Tikkoatokak	Kamanatsuk Brook	56°45'26.58, -62°52'14.21	L	55			1	1	1
F01	Nain	Fraser	56°41'22.74, -63°27'56.10	A				24	2	4
A01	Anaktalik	Anaktalik	56°29'52.47, -62°55'46.86	A				24	2	3
A02	Anaktalik	Anaktalik	56°34'53.08, -63°19'24.07	L		3		22	1	1
V01	Voisey	Kogluktokoluk Brook	56°18'47.06, -62°10'07.13	A	2			22	2	2
V02	Voisey	Kogluktokoluk Brook	56°17'38.10, -62°16'56.08	A				2	2	2
V03	Voisey	Kogluktokoluk Brook	56°17'38.28, -62°23'34.38	A	6			18	2	2
V04	Voisey	Kogluktokoluk Brook	56°16'41.35, -62°25'05.54	A	10			14	2	2
V05	Voisey	Kogaluk River	56°10'13.46, -61°44'40.35	A				1	1	1
V06	Voisey	Kogaluk River	56°09'32.52, -61°45'45.79	A	7			5	1	1
V07	Voisey	Kogaluk River	56°22'08.70, -63°29'30.50	L				14	2	2
V09	Voisey	Kogaluk River	56°40'31.70, -64°00'07.50	L				9	1	1
V10	Voisey	Kogaluk River	56°36'13.70, -63°52'09.10	L				12	2	2
V11	Voisey	Kogaluk River	56°24'56.20, -64°06'08.10	L		1		23	2	2
V13	Voisey	Kogaluk River	56°09'09.70, -63°56'21.20	L				6	1	1
V14	Voisey	Kogaluk River	56°06'38.40, -63°23'18.90	L				17	1	1
V15	Voisey	Kogaluk River	56°02'52.10, -63°35'54.40	L				13	2	2
V16	Voisey	Kogaluk River	55°55'26.19, -63°08'34.22	L				7	2	2
W01	Notakwanon	Notakwanon	55°58'22.05, -61°45'15.82	A	1			3	1	1
W02	Notakwanon	Notakwanon	55°56'00.23, -62°04'15.16	A	6		4	12	1	1
W03	Notakwanon	Notakwanon	55°54'09.81, -62°06'46.41	A	2			8	3	3
W04	Notakwanon	Notakwanon	55°57'55.29, -62°19'28.48	A	1			16	2	2
W05	Notakwanon	Notakwanon	55°54'18.34, -62°59'10.25	A				12	2	2
W06	Notakwanon	Notakwanon	55°49'25.42, -63°03'34.33	A				12	2	2
W09	Notakwanon	Notakwanon	55°23'38.23, -63°16'56.28	L				16	1	1
G01	Rocky Harbour	Rocky Harbour	49°39'39.16, -57°37'31.53	L				4	1	1
G02	Rocky Harbour	Rocky Harbour	49°38'35.39, -57°33'03.40	L				6	2	2

Table 3.1 Continued.

Site	Drainage	Watershed	Latitude, Longitude	Access	Number of *S. fontinalis*	Number of *S. namaycush*	Number of *S. Salar*	Number of *S. alpinus*	Number of *S. alpinus* Lineages	Number of *S. alpinus* Haplotypes
G03	Rocky Harbour	Rocky Harbour	49°37'58.56, -57°35'16.52	L				16	2	4
G04	Rocky Harbour	Rocky Harbour	49°37'39.10, -57°36'49.91	L				12	2	4
G05	Rocky Harbour	Rocky Harbour	49°37'46.22, -57°37'40.93	L				21	1	4
G06	Rocky Harbour	Rocky Harbour	49°37'37.35, -57°41'44.16	L			5			
I01	Eastern Island	Gander	48°56'19.82, -54°41'04.31	L*				22	1	2
I02	Eastern Island	Gander	48°56'19.82, -54°41'04.31	L*				21	2	2
I03	Eastern Island	Wing	48°59'37.79, -54°09'01.97	L*				24	1	1
					143	**5**	**15**	**1133**		

* Gander Lake and Wings Pond maintain sea-access but contain lacustrine residents, these lakes were therefore categorized as “landlocked” for analyses.

3.10 Figures

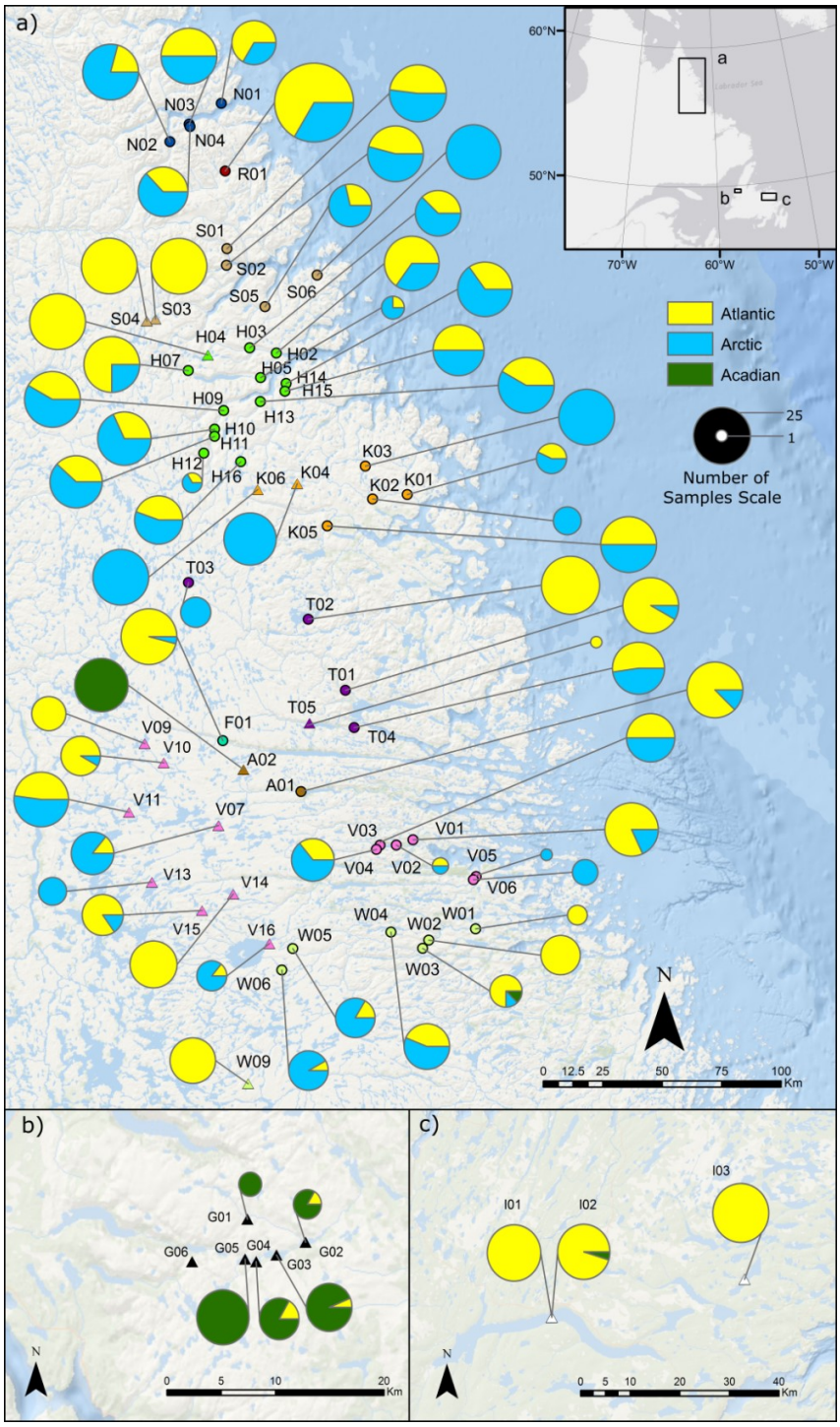

Fig.3.1 Map of sampling locations for Arctic Charr (*Salvelinus alpinus*) in a) Labrador and the b) west and c) east coasts of Newfoundland. Sea-accessible sites are denoted by circles, landlocked sites are denoted by triangles. Sites of the same colour are in the same drainage. Pie charts indicate the number of samples of the Acadian, Atlantic or Arctic lineage observed at a given site and are scaled by sample size. Map created using ArcGIS (ESRI).

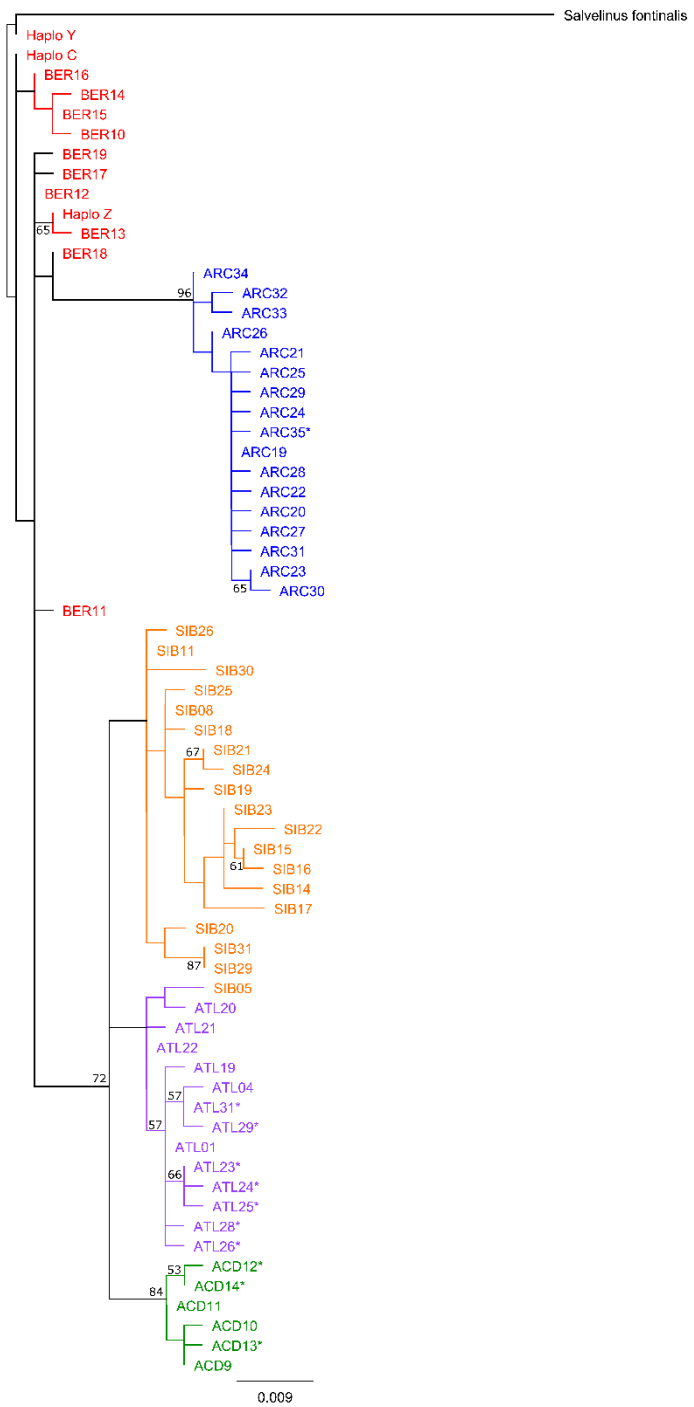

Fig.3.2 Maximum likelihood phylogenetic tree of Arctic Charr (*Salvelinus alpinus*) haplotypes of the mtDNA control region. Tree was generated using PhyML (Guindon and Gascuel 2003) with 1000 bootstrap replicates. Those bootstrap values greater than 50% are shown on the tree. Haplotypes are colour-coordinated by lineage as designated in Moore et al. (2015): blue - Arctic, red - Bering, orange - Siberia, purple - Atlantic, green, - Acadian. New haplotypes identified in this study and Salisbury et al. 2017 are starred.

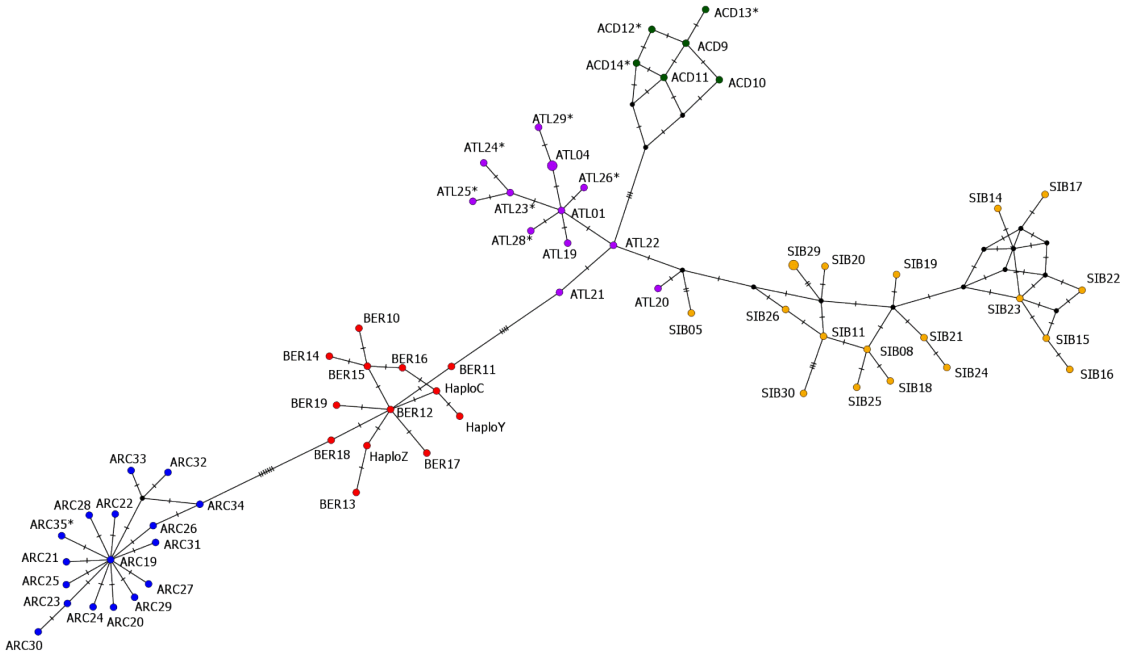

Fig.3.3 Haplotype map of Arctic Charr (*Salvelinus alpinus*) haplotypes created with PopArt version 1.7 (Leigh and Bryant, 2015) using a Median-Joining network (Bandelt et al. 1999) and an Epsilon value of 0. New haplotypes identified in this study and Salisbury et al. 2017 are starred.

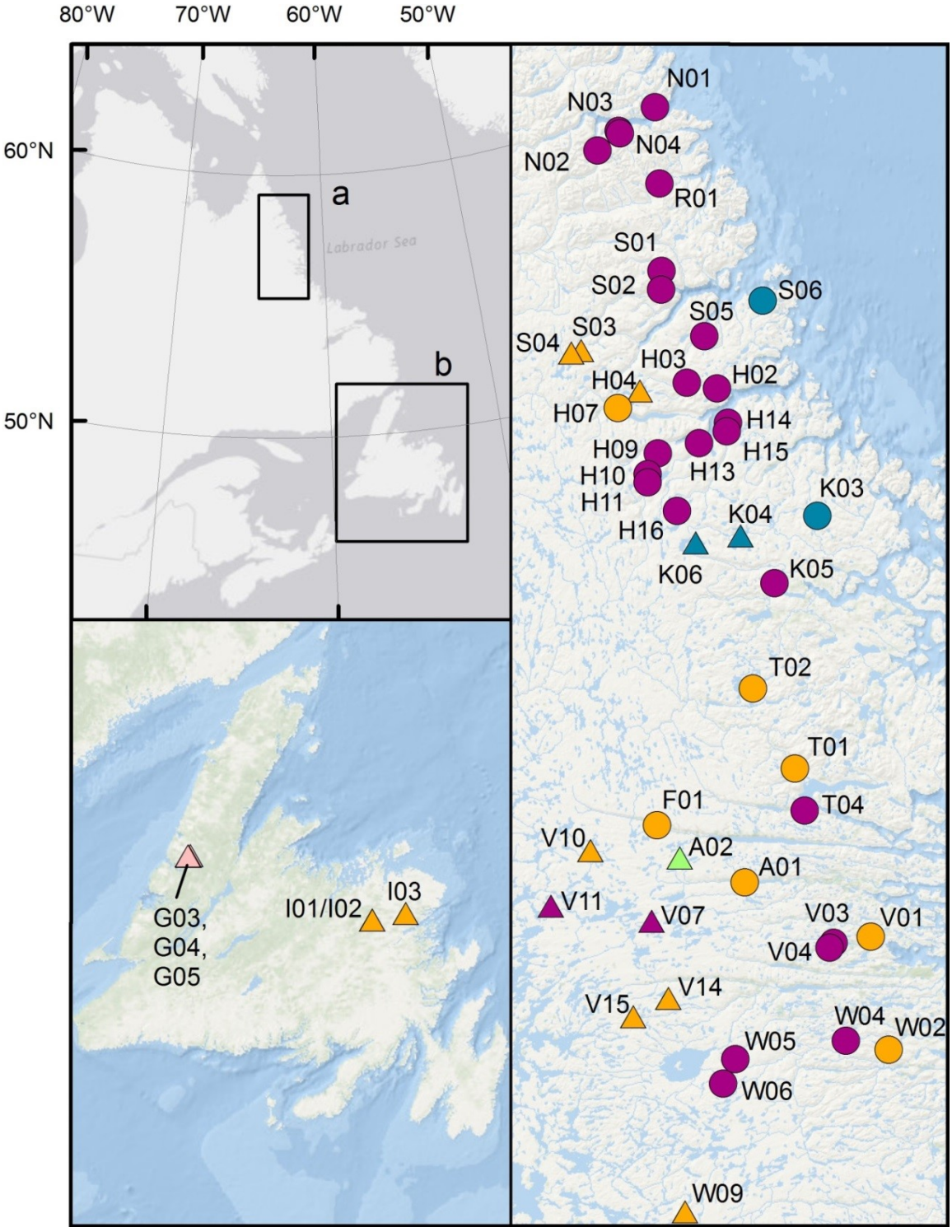

Fig.3.4 Results of SAMOVA analysis when considering all locations in a) Labrador and b) Newfoundland with > 10 samples and taking into account geography of locations using a Delaunay matrix. Locations are coloured by grouping (K = 5). Sea-accessible sites are denoted by circles, landlocked sites are denoted by triangles. Map created using ArcGIS (ESRI).

3.11 Supporting Information

Table S3.1 GenBank accession numbers for all control region haplotypes used in mitochondrial analysis.

Haplotype name	Original source	GenBank accession number
ARC19	Alekseyev et al. 2009	EU310899
ARC20	Moore et al. 2015	KC907317
ARC21	Moore et al. 2015	KC907318
ARC22	Moore et al. 2015	KC907319
ARC23	Moore et al. 2015	KC907320
ARC24	Moore et al. 2015	KC907321
ARC25	Moore et al. 2015	KC907322
ARC26	Moore et al. 2015	KC907323
ARC27	Moore et al. 2015	KC907324
ARC28	Moore et al. 2015	KC907325
ARC29	Moore et al. 2015	KC907326
ARC30	Moore et al. 2015	KC907327
ARC31	Moore et al. 2015	KC907328
ARC32	Moore et al. 2015	KR011244
ARC33	Moore et al. 2015	KR011243
ARC34	Ayers 2010	KR011245
ARC35	New	MK208871
BER10	Alekseyev et al. 2009	EU310900
BER11	Alekseyev et al. 2009	EU310901
BER12	Alekseyev et al. 2009	EU310902
BER13	Alekseyev et al. 2009	EU310903
BER14	Moore et al. 2015	KR011246
BER15	Moore et al. 2015	KR011247
BER16	Ayers 2010	KR011248
BER17	Ayers 2010	KR011250
BER18	Ayers 2010	KR011251
BER19	Moore et al. 2015	KR011249
HaploC	Taylor et al. 2008	KR011254
HaploY	Taylor et al. 2008	KR011253
HaploZ	Taylor et al. 2008	KR011252
SIB5	Brunner et al. 2001	AF298013
SIB8	Brunner et al. 2001	AF298016
SIB11	Alekseyev et al. 2009	EU310907
SIB14	Alekseyev et al. 2009	EU310910
SIB15	Alekseyev et al. 2009	EU310911
SIB16	Alekseyev et al. 2009	EU310912
SIB17	Alekseyev et al. 2009	EU310913
SIB18	Alekseyev et al. 2009	EU310914
SIB19	Alekseyev et al. 2009	EU310915
SIB20	Alekseyev et al. 2009	EU310916
SIB21	Alekseyev et al. 2009	EU310917

Table S3.1 Continued.

Haplotype name	Original source	GenBank accession number
SIB22	Alekseyev et al. 2009	EU310918
SIB23	Alekseyev et al. 2009	EU310919
SIB24	Alekseyev et al. 2009	EU310920
SIB25	Alekseyev et al. 2009	EU310921
SIB26	Alekseyev et al. 2009	EU310922
SIB29	Alekseyev et al. 2009	EU310925
SIB30	Alekseyev et al. 2009	EU310926
SIB31	Moore et al. 2015	KR011255
ATL1	Brunner et al. 2001	AF297991
ATL4	Brunner et al. 2001	AF297994
ATL19	Moore et al. 2015	KR011258
ATL20	Moore et al. 2015	KR011261
ATL21	Moore et al. 2015	KR011257
ATL22	Moore et al. 2015	KR011256
ATL23	Salisbury et al. 2018	MK208872
ATL24	Salisbury et al. 2018	MK208873
ATL25	Salisbury et al. 2018	MK208874
ATL26	New	MK208875
ATL28	New	MK208876
ATL29	New	MK208877
ATL31	New	MK208878
ACD9	Alekseyev et al. 2009	EU310898
ACD10	Moore et al. 2015	KR011259
ACD11	Moore et al. 2015	KR011260
ACD12	New	MK208868
ACD13	New	MK208869
ACD14	New	MK208870
S. fontinalis	Keskin, E. (GenBank only)	HQ167705
S. namaycush	Taylor et al. 2008	KT362731
S. salar	Oleinik, A.G. (GenBank only)	KY122303

Table S3.2 *Salvelinus alpinus* D-loop haplotypes observed in sampling locations.

Site	ACD9	ACD11	ACD12	ACD13	ACD14	ATL01	ATL04+ ATL31	ATL04	ATL31	ATL01 or ATL04	ATL19	ATL23	ATL24	ATL25	ATL26	ATL28	ATL29	ARC19 + ARC19 or ARC24	ARC19	ARC19 or ARC24	ARC20	ARC22	ARC35
N01						9											1	5		5			
N02						5												19	1	18			
N03						10	2	1	1									12	1	11			
N04						7												12	1	11			
R01						31	1		1									15	1	14		1	
S01						12												13	1	12			
S02						9	1		1			1						13	1	12			
S03												24											
S04												22	1	1									
S05						3	1	1										10		10			
S06																		23	1	22			
H02						11	4	3	1									8	1	7			
H03						5	1		1									10	2	8			
H04						24																	
H05							1	1										3		3			
H07						18												6	1	5			
H09						10												14	1	13			
H10						7												15		15			
H11						7	1		1									13	1	12			
H12						1												2		2			
H13						10												14	1	13			
H14						7	1		1									15	1	14			
H15						10												10	1	9			
H16						8												10		10			
K01						3												4	1	3			
K02																		6	1	5			
K03																		24	1	23			
K04																		20		20	1		
K05						11	1		1									12	1	11			
K06																		24		24			
T01						17	4	3	1							1		1	1				1
T02						25										1							
T03																		7		7			
T04						11												10	1	9			
T05						1																	
F01						15	7	7								1		1		1			
A01						20									1			3	1	2			

Table S3.2 Continued.

Site	ACD9	ACD11	ACD12	ACD13	ACD14	ATL01	ATL04+ ATL31	ATL04	ATL31	ATL01 or ATL04	ATL19	ATL23	ATL24	ATL25	ATL26	ATL28	ATL29	ARC19 + ARC19 or ARC24	ARC19	ARC19 or ARC24	ARC20	ARC22	ARC35
A02	22																						
V01						18												4	1	3			
V02						1												1	1				
V03						9												9		9			
V04						5												9	1	8			
V05																		1	1				
V06																		5	1	4			
V07						1				1								12		12			
V09						9																	
V10						11												1		1			
V11						11												12		12			
V13																		6		6			
V14						15				2													
V15						9				2								2		2			
V16						1												6		6			
W01						3																	
W02						12																	
W03	1					6												1	1				
W04						7												9		9			
W05						2												10		10			
W06						1												11		11			
W09						16																	
G01	4																						
G02	5					1																	
G03	11	3			1	1																	
G04	7	2	1			2																	
G05	11	6	3	1																			
G06																							
I01						21					1												
I02	1					20																	
I03						24																	
Total	**62**	**11**	**4**	**1**	**1**	**513**	**25**	**16**	**9**	**5**	**1**	**47**	**1**	**1**	**1**	**3**	**1**	**453**	**29**	**424**	**1**	**1**	**1**

3.11.1 SAMOVA Results

When geography was not considered in the SAMOVA model for all sampling locations, F_{CT} was maximized for K = 4 (Fig.S3.1a). The first grouping was identical to the first grouping when considering geography but did not contain the populations V07 or W06 (Fig.S3.2b). These two sampling locations were composed of predominately of Arctic lineage individuals and were instead grouped with the 4 Labrador populations containing only Arctic lineage individuals (S06, K03, K04, K06). The third group contained A02 with the populations from the west coast of Newfoundland. The fourth group was identical to the fourth group when geography was considered.

SAMOVA analyses of only the Labrador populations found F_{CT} was maximized for K = 6 for the geography-dependent model. However, the difference in F_{CT} between K = 6 and K = 4 was 0.08 and plots of F_{CT} versus K revealed that F_{CT} leveled off at K = 4(Fig.S3.1b). Given this small difference in F_{CT} we report the more parsimonious results of K = 4 here. The first group contained 27 locations and was nearly identical to that of the full model considering geography but also included H07 (Fig.S3.2c). The second group contained the four all-Arctic lineage populations. The third group contained 13 locations containing predominately Atlantic lineage samples. The final group was composed of A02.

SAMOVA analyses of only the Labrador populations found F_{CT} was maximized for K = 5 for the geography-independent model (Fig.S3.1b). However, the difference in F_{CT} between K = 5 and K = 4 was 0.07 and plots of F_{CT} versus K revealed that F_{CT} leveled off at K = 4 (Fig.S3.1b). Given this small difference in F_{CT} we report the more parsimonious results of K = 4 here. The groupings were identical to the geography-independent model except W06 was grouped with the four all-Arctic populations (Fig.S3.2d).

SAMOVA analyses of only the Newfoundland populations found K = 2 to maximize F_{CT} using both the geography-dependent and geography-independent models (Fig.S3.1c). Both models separated the east coast populations from the west coast populations (Fig.S3.2e,f).

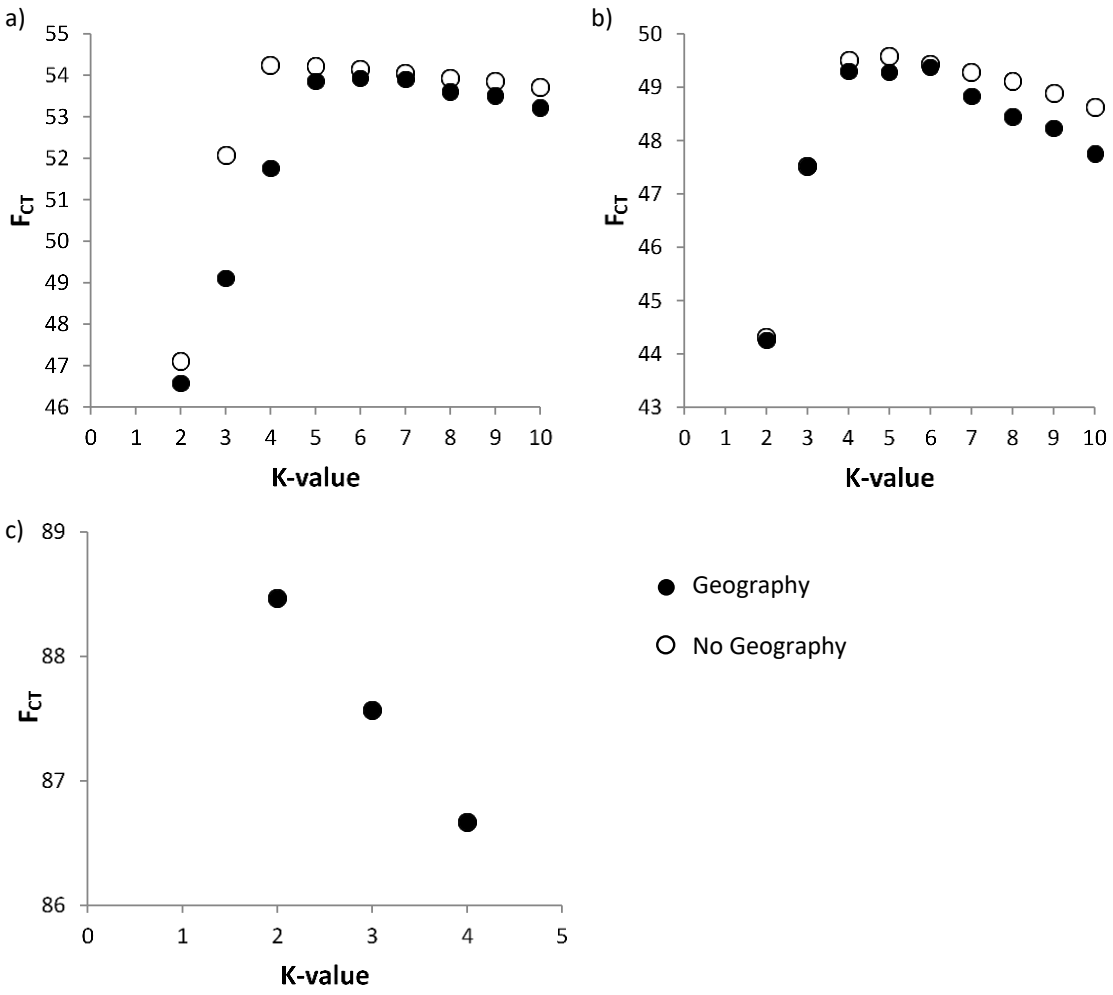

Fig.S3.1 F_{CT} versus K-value for SAMOVA analyses of a) all sampling locations, b) only Labrador sampling locations, c) only Newfoundland sampling locations. Filled circles indicate SAMOVA analyses for which geography was taken into account using a Delaunay matrix, open circles indicate SAMOVA analyses for which geography was not taken into account.

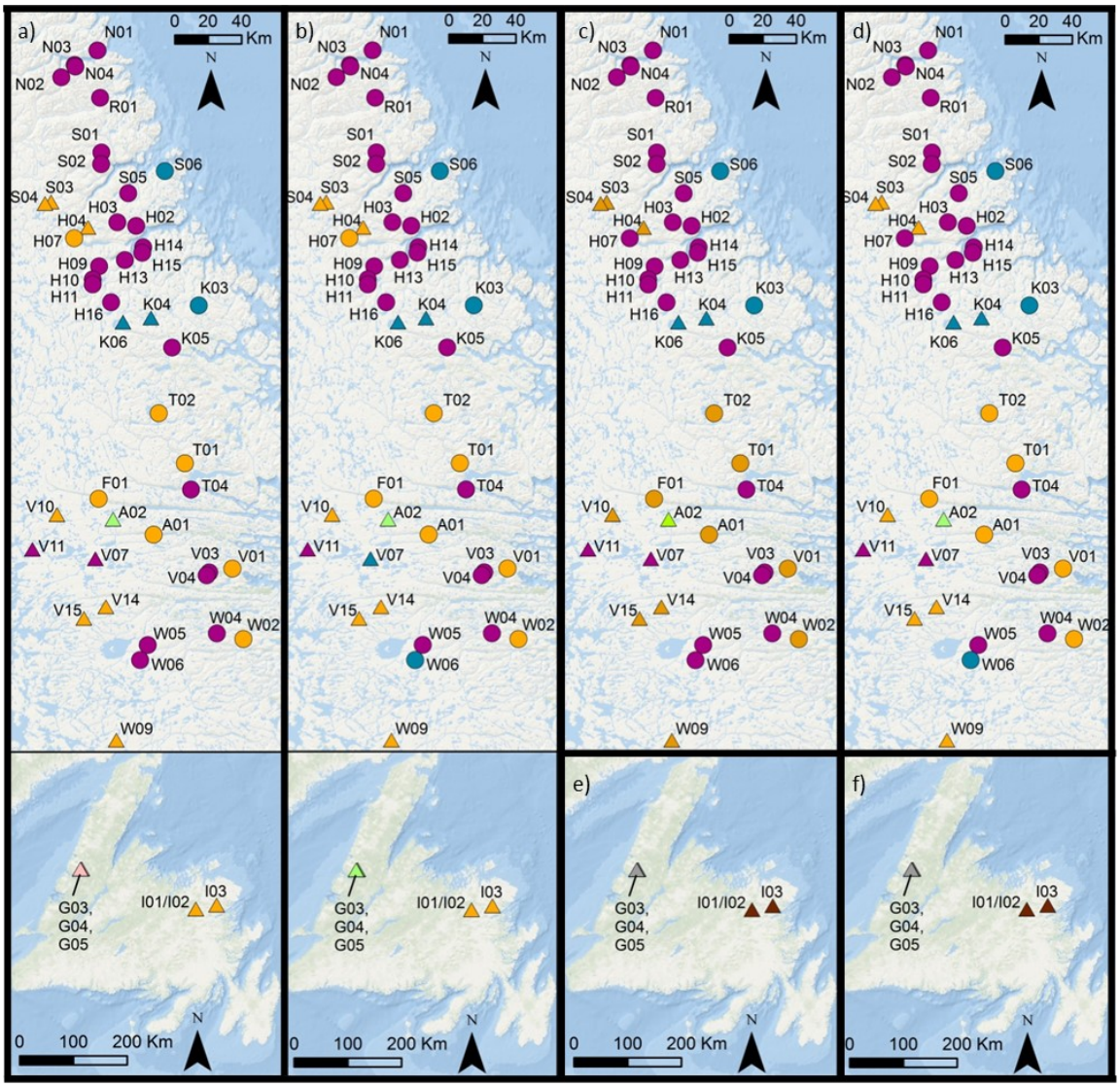

Fig.S3.2 Results of SAMOVA analyses for all sampling locations a) with (K = 5) and b) without (K = 4) the consideration of geography; for only Labrador sampling locations c) with (K = 4) and d) without (K = 4) the consideration of geography; for only Newfoundland sampling locations e) with (K = 2) and f) without (K = 2) the consideration of geography. Locations are coloured by grouping. Sea-accessible sites are denoted by circles, landlocked sites are denoted by triangles. Map created using ArcGIS (ESRI).

3.12 References

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CHAPTER 4 - LIMITED GENETIC PARALLELISM UNDERLIES RECENT, REPEATED INCIPIENT SPECIATION IN GEOGRAPHICALLY PROXIMATE POPULATIONS OF AN ARCTIC FISH (*SALVELINUS ALPINUS*)

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4.1 Abstract

The genetic underpinnings of incipient speciation, including the genomic mechanisms which contribute to morphological and ecological differentiation and reproductive isolation, remain poorly understood. The repeated evolution of consistently, phenotypically distinct morphs of Arctic Charr (*Salvelinus alpinus*) within the Quaternary period offer an ideal model to study the repeatability of evolution at the genomic level. Sympatric morphs of Arctic Charr are found across this species' circumpolar distribution. However, the specific genetic mechanisms driving this morph differentiation are largely unknown despite the cultural and economic importance of the anadromous morph. We used a newly designed 87k SNP chip to investigate the character and consistency of the genomic differences among sympatric morphs within three recently deglaciated and geographically proximate lakes in Labrador, Canada. We found genetically distinguishable small and large morph Arctic Charr in all three lakes consistent with resident and anadromous morphs, respectively. A degree of reproductive isolation between sympatric morphs is likely given genome-wide distributions of outlier SNPs and high genome-wide F_{ST}s. Across all lakes, outlier SNPs were largely non-overlapping suggesting a lack of genetic parallelism driving morph differentiation. Alternatively, several genes and paralogous copies of the same gene consistently differentiated morphs across multiple lakes suggesting their importance to the manifestation of morphs. Our results confirm the utility of Arctic Charr as a model for investigating the predictability of evolution and support the importance of both genetic parallelism and non-parallelism to the incipient speciation of Arctic Charr morphs.

4.2 Introduction

A fundamental question in evolutionary biology concerns the degree to which evolution can be considered repeatable (Elmer and Meyer 2011). Instances of recent and repeated phenotypic differentiation provide a unique opportunity to investigate the predictability of evolution (Coyne and Orr 2004; Rundle and Nosil 2005) by allowing for the detection of the genomic mechanisms driving incipient divergence before they have been erased by subsequent selection and drift (Hodges and Derieg 2009). Common genomic regions that are consistently subject to divergent selection between phenotypically distinct morphs across "natural replicate" populations can be considered as evidence of parallelism (Deagle et al. 2012; Hohenlohe et al. 2010; Ravinet et al. 2017). They are powerful models for empirically testing Gould's (1990) "tape of life" thought experiment (Blount et al. 2018; Elmer et al. 2014).

There has been little consensus as to the expected degree of genetic parallelism associated with phenotypic divergence despite study of several species exhibiting "natural replicates". Some repeated morphological radiations demonstrate a complete absence of parallelism at the genetic level, as was the case for cichlids in isolated Guatemalan crater lakes (Elmer et al. 2014; Kautt et al. 2012). Alternatively, structural variation, population history, and geography have been shown to affect rates of genomic parallelism (e.g., Kess et al. 2018; Le Moan et al. 2016; Morales et al. 2019; Rougemont et al. 2017) and a meta-analysis of radiation studies found an 80% predicted chance of gene reuse in recently diverged populations (Conte et al. 2012).

The degree of parallelism contributing to morph differentiation has been observed to increase from the genomic level, to the transcriptomic level, to the morphological level (Jacobs et al. 2020; Roda et al. 2013). Also, while both paralogs and homeologs have been proposed as a potentially important source of phenotypic diversity, their contribution to the evolution of repeated morph differentiation remains largely unknown (Conte et al. 2012; Nichols et al. 2008; Rosenblum et al. 2014). If paralogs maintain similar functionality, divergent selection upon different paralogous copies might facilitate parallel morph differentiation in replicate populations, particularly within those species having undergone a recent whole genome duplication (Macqueen and Johnston 2014).

Arctic Charr (*Salvelinus alpinus*) exhibit repeated natural replicate morph radiations across their Holarctic distribution with up to six morphs described living in sympatry (Doenz et al. 2019). Morphs can differ in morphology, life history, behaviour, and ecology, and they are generally associated with similar ecological conditions across replicate populations (Jonsson and Jonsson 2001; Klemetsen 2010). Like all salmonids, the species has recently undergone a whole genome duplication ~88 mya (Macqueen and Johnston 2014) and therefore constitutes an ideal model for studying genomic parallelism at the level of the paralog. Studies investigating the genetic differentiation among sympatric Arctic Charr morphs (e.g., Gíslason et al. 1999; Gomez-Uchida et al. 2008; Gordeeva et al. 2015) examined sympatric morphs using a few neutral markers and only within landlocked populations (i.e., populations residing in lakes which are separated from the sea by a physical barrier preventing migration) (but see Guðbrandsson et al. 2019; Jacobs et al. 2020). Therefore, the adaptive differentiation among morphs in sea accessible environments, where anadromous and resident individuals may coexist, and the degree to which such adaptive differentiation exhibits evidence of parallelism is largely unexplored in this species.

Sympatric resident and anadromous morphs have been less studied than their landlocked counterparts. Anadromous smolts and adults make annual migrations to the ocean during the summer months to feed, before returning to fresh water to overwinter (Dempson and Green 1985; Klemetsen et al. 2003; LeDrew 1980). Residents remain in fresh water their entire lives; they mature at a younger age and smaller size and also achieve a smaller lifetime length than the anadromous morph (Jonsson and Hindar 1982; Jonsson and Jonsson 2001; Rikardsen et al. 2004). While residency and anadromy have been thought to be primarily plastic traits in Arctic Charr (Jonsson and Jonsson 2001; Moore et al. 2014; Nordeng 1983) recent evidence based on neutral markers suggests that sympatric resident and anadromous morphs may be genetically differentiated (Doenz et al. 2019; O'Malley et al. 2019; Salisbury et al. 2018). Given that the anadromous morph forms the basis of economically and culturally important subsistence, recreational, and commercial fisheries often run by Indigenous peoples (Moore et al. 2013; Scott and Crossman 1973) an understanding of the genetic contribution to Arctic Charr life history is essential for management and conservation.

Here we used an 87k Arctic Charr SNP array (Nugent et al. 2019) to examine the genetic differentiation between Arctic Charr morphs inhabiting three sea-accessible lakes in Labrador. One of these lakes (Ramah Lake) has previously been shown to harbour genetically distinguishable small (putatively resident) and large (putatively anadromous) Arctic Charr based on neutral microsatellites (Salisbury et al. 2018). Our first objective was to examine whether similar evidence of genetic sub-structuring associated with size differences was also found in two nearby sea-accessible lakes in Labrador. Second, we aimed to identify the outlier genes differentiating morphs. Our third objective was to assess for genetic parallelism of morph differentiation across populations. This system is an ideal model to detect parallelism given that the evolution of sympatric morphs likely occurred < 9000 years ago after the deglaciation of Labrador (Bryson et al. 1969; Occhietti et al. 2011). The recent evolution of morphs in this system suggests that parallel genomic signatures of incipient speciation are less likely to have been erased due to subsequent drift and selection (Hodges and Derieg 2009). Furthermore, the historical colonization and introgression of three glacial lineages within Labrador (Brunner et al. 2001; Moore et al. 2015; Salisbury et al. 2019), the contemporary high gene flow among populations (Bernatchez et al. 1998; Layton et al. 2020; Salisbury et al. 2018), and the geographic proximity of the three lakes studied here all likely contributed to their shared ancestral genetic variation. Given this anticipated genetic similarity and barring a high degree of genetic drift between populations we therefore expected a high degree of genetic parallelism if sympatric morph differentiation was observed in multiple populations (Conte et al. 2012; Roda et al. 2013; Westram et al. 2016).

4.3 Methods

4.3.1 Sampling

Sampling was conducted in collaboration with the Department of Environment and Conservation of Newfoundland and Labrador using variable sized standardized nylon monofilament gillnets (1.27–8.89 cm diagonal) from Labrador lakes in 2014 and 2015. Tissue samples (gill and fin) were collected, and fish were weighed, measured (fork length, FL) in mm, and assessed for sex and maturity. We noticed samples from three lakes (Ramah Lake, Esker North Lake, and Brooklyn Lake) (Fig.4.1, Table S4.1)

included mature fish at a variety of fork lengths suggesting the presence of multiple morphs. These observed size differences in mature fish, in addition to the fact that all three lakes were sea-accessible (Anderson, 1985), suggested the potential for resident and anadromous morphs in these lakes since anadromous charr are known to mature at a larger size and achieve a greater lifetime size than resident charr (which are typically < 200 mm) (Kristoffersen et al. 1994). We therefore selected individuals of varying lengths and of both sexes and differing maturity statuses (mature and immature) from all three lakes for downstream analysis to investigate for the presence of genetically distinguishable morphs.

4.3.2 Extraction, Sequencing, Genotyping and Quality Control

Individuals from these three lakes (N_{total} = 181) were digested at 55°C for approximately eight hours using Proteinase K (Bio Basic Inc., Markham, ON, Canada). DNA was extracted using either a glassmilk protocol modified from Elphinstone, Hinten, Anderson, and Nock (2003) or a Phenol Chloroform protocol modified from Sambrook and Russell (2006). A Multiprobe II plus liquid handling system (Perkin Elmer, Waltham, MA, USA) was used to extract DNA for those individuals processed with the modified glassmilk protocol. DNA concentrations were quantified using QuantIT PicoGreen (Life Technologies) on the LightCycler 480 II (Roche) and normalized using epMotion 5075 liquid handling robot (Eppendorf).

DNA samples (N = 61, 60, 60 from Ramah, Brooklyn, and Esker North lakes, respectively; Table S4.1) were genotyped at the Clinical Genomic Centre of Mount Sinai Hospital (Toronto, Canada) using an 87k Affymetrix Axiom Array (Nugent et al. 2019). Resulting CEL genomic data files for each sample were analyzed using Axiom Analysis Suite (Version 4.0.1.9) using the "best practices workflow" for a diploid organism (for details please see Supporting Information). A minor allele frequency (MAF) filter of 0.01 was applied to each location using PLINK (Version 1.9)(Chang et al. 2015). PGDSpider (Version 2.1.1.5)(Lischer and Excoffier 2011) was used to convert between PLINK and Genepop files and the R package (R Core Team 2013) *genepopedit* (Stanley et al. 2017) was used to order and arrange Genepop files for downstream analyses.

After filtering out poor quality individuals we retained for further analyses: N = 60 from Ramah, N = 58 from Brooklyn, N = 60 from Esker North (Table S4.1). Overall, N = 321 SNPs were removed from the analysis due to inconsistent scoring among replicate samples leaving N = 62812 high-quality polymorphic and monomorphic SNPs for all three locations. After MAF filtering, 22603, 14404, 16084 SNPs remained for Ramah, Brooklyn, and Esker North, respectively (13041 SNPs were overlapping in all three locations, Fig.S4.1). The loss of SNPs from the original 87k on the SNP array may reflect ascertainment bias given that the array was designed based on wild Icelandic populations and several aquaculture lineages. However, one of these aquaculture lineages was sourced from Fraser River, Labrador in relatively close proximity to our sampling locations.

4.3.3 Population Structure Analyses

We used ADMIXTURE (Version 1.3) (Alexander et al. 2009) to test for evidence of genetic sub-structuring within each lake population. Each lake was assessed for K = 1-5 with 10 cross-validations. Individuals within each lake were assigned to genetic groups based on Q-values for the best K-value (that with the lowest average cross-validation error). Methods for additional population structure analyses (FASTSTRUCTURE (Raj, Stephens, and Pritchard, 2014), *PCAdapt* (Version 4.1.0) (Luu et al. 2017), DAPC using the R package *Adegenet* (Jombart 2008), *snmf* (Frichot and François 2015) are outlined in the Supporting Information. PLINK was used to estimate: linkage disequilibrium r2 values between all SNP pairs (within a single linkage group) for each lake, Weir and Cockerham (1984) F_{ST} between sympatric genetic groups, and mean observed and expected heterozygosities (H_O, H_E) for each genetic group. We performed two-way ANOVA of the effect of the interaction of genetic group assignment and maturity on fork length (mm). A posthoc Tukey's test was used to statistically compare genetic group/maturity combinations.

The population structure among all samples from all lakes was assessed based on 21404 SNPs retained after a MAF filter of 0.01 across all lake samples. A hierarchical AMOVA was conducted using the R package *poppr* (Kamvar et al. 2014) to assess the relative contributions to genetic variation of morph type nested within lake location. A

neighbour-joining tree was constructed using uncorrected (p) distances and visualized using the program SplitsTree4 (Huson and Bryandt 2006). Pairwise Weir and Cockerham (1984) F_{ST} estimates among genetic groups detected within all three lakes were obtained using the R package *hierfstat* (Goudet 2005).

4.3.4 Outlier Detection

Three outlier detection methods were used to identify outlier SNPs between genetic subgroups detected using the population structure analyses above. Given that each method uses a different mechanism to detect putative signatures of selection, the use of multiple outlier detection methods was justified to maximize our potential for discovering SNPs demonstrating parallelism across lakes. First, the R package *PCAdapt* was also used to conduct a PCA using K = 1 (since population structure analyses only suggested a maximum of two morphs in each lake, see below) with the default Mahalanobis distance. Outlier SNPs were identified as those that significantly correlated with the first PC after p-values were corrected using the False Discovery Rate (FDR, Storey and Tibshirani 2003) with the R package *qvalue* (Storey 2015). Second, using the F_{ST}s estimated from PLINK, those SNPs with an F_{ST} > 3 SD above the mean F_{ST} for a given lake were considered outliers. Third, a redundancy analysis (RDA) was used to detect SNPs associated with four morphological measurements (length, weight, maturity, sex) in each lake using the R package *vegan* (Oksanen et al. 2013). For RDAs, missing genotypes were replaced by the most common allele for a given locus and samples with missing morphological data were removed from the analysis. An ANOVA like permutation test was conducted to assess the significance of all constrained axes, each individual axis, and all variables (length, weight, maturity, sex) in explaining the genotype data using 999 permutations with the *anova.cca* function from the R package *vegan*. Constrained axes with significant effects were investigated for outlier SNPs, defined as those SNPs with scores > 3 SD from the centre of the axis. SNPs detected as an outlier by any of the three methods were combined to create a list of outliers differentiating morphs for each lake. Outlier SNPs were assigned to the closest gene (that were assigned GO terms) within 5000 bp, based on the recently released charr genome (Christensen et al. 2018).

The R package *VennDiagram* (Chen and Boutros 2011) was used to visualize outlier SNPs by lake. Outlier SNPs detected in two or more lakes were considered candidates for parallel selection. These outlier SNPs were visualized using the R package *ComplexHeatMap* (Gu et al. 2016) to assess if they demonstrated parallel direction of selection. SNPs identified as outliers in any test were removed, and the ADMIXTURE analyses were conducted again for each lake using this set of putative "neutral" SNPs.

4.3.5 Identifying Parallel Paralogs

We investigated whether there was evidence for divergent selection of paralogous genes among morphs both within and among lakes by comparing the annotated gene names associated with outlier SNPs. Outlier genes annotated with identical gene names but different protein codes ("XP_") were considered paralogs. While this approach is limited to detecting only those paralogs included on the SNP chip and does not take into account the phylogenetic relationship among paralogs it still provides an insight into whether paralogous copies of the same gene may contribute to local adaptation or incipient divergence. We therefore identified instances where multiple paralogs showed evidence of divergent selection between morphs within a single lake and instances where different paralogs showed evidence of divergent selection between morphs in different lakes.

4.3.6 Gene Ontology Enrichment

Gene Ontology (GO) enrichment analyses for Biological Processes were conducted using the R package *TopGO* employing the protein GO annotation file generated for charr by Christensen et al., (2018) and formatted using BEDOPS (Neph et al., 2012). GO term significance was assessed with a Fisher's exact test using the "weight01" algorithm, p-values were corrected using FDR ($\alpha = 0.05$). GO analyses were conducted for 1) all outlier SNPs detected in any lake, with any method, and 2) those outlier SNPs detected in two or more lakes. The GO term universe for each analysis was limited to those SNPs located < 5000 bp from a gene and consisted of 1) those SNPs which passed filtering in at least one lake location, and 2) those SNPs which passed filtering in at least two lake locations.

4.4 Results

All population structure analyses identified K = 2 genetic groups in Ramah, Esker North, and Brooklyn lakes. Assignment of individuals to genetic groups was identical across all population structure analyses. We therefore discuss only the ADMIXTURE results (Fig.4.2 a, d, g) and have reported the others in the Supporting Information (Table S4.2 – S4.4, Fig.S4.2 – Fig.S4.7). High Q-values indicated strong support for genetic assignment, although six individuals in Esker North had intermediate Q-values (0.2 < Q-value < 0.8), suggesting the potential for hybrids in this location. These six individuals were removed before conducting the PCAdapt and F_{ST} outlier detection analyses for Esker North but were retained in the analysis for the RDA (which, unlike the other techniques, exploits phenotypic data to find outliers and was appropriate for the hybrids given their intermediate lengths as seen see below). Pairwise F_{ST} between ADMIXTURE-defined genetic groups was lowest in Esker North (excluding hybrids, mean F_{ST} = 0.06, weighted F_{ST} = 0.08), intermediate in Ramah (mean F_{ST} = 0.08, weighted F_{ST} = 0.11) and highest in Brooklyn (mean F_{ST} = 0.14, weighted F_{ST} = 0.20). These relatively high F_{ST} values suggest the potential for genetic drift among sympatric morphs, further supported by linkage disequilibrium decay plots, particularly in Ramah and Brooklyn lakes (Fig.S4.8). Observed and expected heterozygosities were generally consistent across lakes and morphs (Table 4.1). Population assignment by ADMIXTURE for all lakes was unchanged after removing outlier SNPs detected within each lake by any method (Table S4.5, Fig.S4.9).

ANOVAs comparing the variation in length with both maturity (2 levels: mature or immature) and ADMIXTURE-assigned genetic group (2 levels) revealed that in all three lakes, one genetic group was significantly shorter than the other ($F_{(1,56)}$ = 221.4, $F_{(1,54)}$ = 630.9, $F_{(1,50)}$ = 245.3, for Ramah, Brooklyn and Esker North (excluding hybrids) respectively, all p-values < 0.001)(Fig.4.2 b, e, h, Table 4.1). We refer to these two genetically distinguishable and size-differentiated groups of samples as the “small” and “big” morphs, henceforth. The average (median) lengths of six putative hybrids in Esker North were 190 mm (191.5 mm), intermediate to those of the remaining “purebred” morphs (Fig.4.2h, Table 4.1). Both morphs contained both mature and immature individuals of both sexes in all lakes (Table 4.1).

Comparisons of morphs across all samples revealed that sympatric morphs were more genetically similar than allopatric morphs of the same type. A neighbour-joining tree comparing all lakes revealed individuals grouped primarily by location, and secondarily by morph type within each lake (Fig.4.3). AMOVA results reveal that 9.1% of genetic variation was found between lakes versus 11.4% between morphs within lakes (Table S4.6). Weighted pairwise F_{ST}s were lower between morphs within lakes than between morphs of the same type from different lakes (Table S4.7).

For all three lakes, the full RDA model (using sex, length, weight, and maturity as variables) as well as just the first RDA axis significantly explained the variance in the genetic data (all axes: $F_{(4,54)} = 1.9$, $F_{(4,53)} = 2.1$, $F_{(4,55)} = 1.5$, for Ramah, Brooklyn and Esker North, respectively, all p-values < 0.001; first RDA axis: $F_{(1,54)} = 4.5$, $F_{(1,53)} = 5.0$, $F_{(1,55)} = 2.8$, for Ramah, Brooklyn and Esker North, respectively, all p-values < 0.001; Tables S4.8-S4.16). The first RDA axis was most closely associated with fish length (Fig.S4.10, Fig.S4.11), which was the variable that explained the most variance in all three lakes ($F_{(1,54)} = 4.4$, $F_{(1,53)} = 3.3$, $F_{(1,55)} = 2.3$, for Ramah, Brooklyn and Esker North, respectively, all p-values < 0.001; Table S4.10, S4.13, S4.16). Given that the first RDA explained nearly half or more than half of the genetic variance in all three lakes (58%, 61%, 46%, for Ramah, Brooklyn, and Esker North, respectively) outlier SNPs were only assessed based on this axis in all three lakes.

The number of outlier SNPs detected between sympatric morphs (combined from all three outlier detection methods), was similar for each of the three lakes (N = 482, 437, 315 in Ramah, Brooklyn, Esker North, respectively) (Fig.4.4a, Fig.S4.12). Some outlier SNPs detected for a given lake were non-polymorphic in other lakes (Table S4.17). Outlier SNPs were detected in 37, 34, and 34 linkage groups in each of Ramah, Brooklyn, Esker North, respectively. No significant Biological Processes GO terms were enriched among all detected outlier SNPs after adjusting p-values using FDR (Table S4.18).

Only 38 (38/1195 = 3%) outlier SNPs were found in common among two or more lakes only one of which was detected in all three lakes (Fig.4.4a). Of these 38 outlier SNPs, 28 (28/1195 = 2% of all outlier SNPs), including the single SNP detected as an outlier in all three lakes (Fig.4.4b), showed evidence of parallel allelic trends (i.e., the

difference in major allele frequency between big and small morphs was in the same direction (positive or negative) for all sympatric morph pairs for which a SNP was detected as an outlier). The 38 outlier SNPs detected in two or more lakes corresponded to 18 genes (Table 4.2). Three additional genes were found to contain two outlier SNPs, each of which were detected as outliers in different lakes for a total of 21 outlier genes detected in two or more lakes (Table 4.2, Fig.4.4a). The SNP detected as outlier in all three lakes was found in the coding region of pappalysin-2. No significant Biological Process GO terms were enriched among outlier genes detected in two or more lakes after adjusting p-values using FDR (Table S4.19).

Evidence of paralogous copies of the same gene containing outlier SNPs was found both within and across lakes. Within Ramah, Brooklyn, and Esker North Lakes, respectively, N = 2, 7, 2 genes were found to contain outlier SNPs in two or more paralogous copies (Table S4.20). For N = 16 genes, different lakes demonstrated outlier SNPs in different paralogous copies of the same gene (Table S4.21). Only two of these genes (pappalysin-2 and pro-neuregulin-3 membrane-bound) had at least one paralog copy detected as an outlier in all three lakes.

For some of these genes, paralogous copies containing outliers were unmapped (Table S4.20, Table S4.21). However, some paralogous copies containing outliers were located on the same chromosome, or on different chromosomes (Table S4.20, Table S4.21). For those paralogous copies found on different chromosomes, many were detected on homeologous chromosomes which are derived from a common pre-salmonid ancestral chromosome that underwent a whole genome duplication. For those 11 genes where different paralogous copies of the same gene were found to contain outlier SNPs in the same lake population, 2 had paralogs on homeologous chromosomes. For those 16 genes where different outlier paralogs were detected in different populations, 7 had paralogs on homeologous chromosomes.

4.5 Discussion

Our results suggest the presence of genetically and phenotypically distinct, sympatric Arctic Charr morphs in three lakes in Labrador, Canada. The genome-wide distribution of outlier loci and high pairwise F_{ST} values support a degree of reproductive

isolation between morphs in each of the three lakes, despite the recent evolution of morphs (<9000 years). However, the hybrids and lower genome wide F_{ST}s observed in Esker North suggest reproductive isolation is incomplete in this lake. We also confirm the presence of genetically distinguishable morphs in Ramah detected previously using microsatellites (Salisbury et al., 2018). Genetic structure was driven primarily by location followed by morph type, as observed in other salmonid species (e.g., Larson et al. 2019; Piette-Lauzière et al. 2019; Prince et al. 2017), suggesting the relative evolutionary independence of morph radiations (Elmer and Meyer 2011).

The size differences among morphs and their presence in sea-accessible lakes (according to Anderson 1985) are consistent with the presence of resident and anadromous morphs. These results contrast with the suggestion that anadromy is a plastic trait in charr (Moore et al. 2014; Nordeng 1983) and has implications for the anadromous charr fishery in Labrador (Andrews and Lear 1956; Dempson et al. 2008; DFO 2001), suggesting the need for independent management of morphs. The outlier genes we detected may be useful candidates to select against undesirable small body size in an aquaculture setting (Yossa et al. 2019). Given that increases in temperature and terrestrial primary productivity driven by climate change are expected to favour residents (Finstad and Hein 2012; Reist et al. 2006), the outlier genes detected here also have practical applications towards the conservation of the anadromous morph.

4.5.1 Drivers and Maintenance of Morph Genetic Differentiation

A comparison of the locations in which sympatric resident and anadromous Arctic Charr are and are not genetically distinguishable could yield insights into the ecological factors driving genetic differentiation. Significant genetic differences have been observed among resident and anadromous Arctic Charr in Labrador (this study and Salisbury et al. 2018), Greenland (Doenz et al. 2019) and Svalbard (O'Malley et al. 2019) but not Baffin Island (Moore et al. 2014). Distance to the ocean and the associated migratory fitness costs (Finstad and Hein 2012) may play a role in favouring genetically distinguishable residents as Baffin Island sites were < 1 km from the ocean (Loewen et al. 2010) whereas the Labrador sites were all > 10 km from the ocean (Ramah ~10 km, Brooklyn ~35 km, Esker North ~78 km, as measured using Google Earth Pro (GEP)). However, genetically

distinguishable morphs in Svalbard (O'Malley et al. 2019) were only ~ 2 km (measured with GEP) from the ocean. The small size of Ramah Lake (0.25 km^2, measured with GEP) also suggests that lake size did not prevent the genetic differentiation of morphs in the similarly sized Baffin Island lakes (0.15 – 1.2 km^2) (Loewen et al. 2009). Alternatively, if Baffin Island was colonized after Labrador despite contemporaneous deglaciation of both regions ~ 9000 BP (Bryson et al. 1969; Occhietti et al. 2011), genetic differences among morphs in Baffin Island may not have had time to become apparent. In addition, although the period anadromous charr spend at sea each year can vary from year to year and across the species' range (e.g., Dempson and Green 1985; Gilbert et al. 2016; Gulseth and Nilssen 2000), longer and more stable anadromous periods might allow for discrete morph spawning times, leading to isolation by time (Hendry and Day 2005). In support of this hypothesis is the differences in egg turgency observed between small and large mature females in Ramah Lake (Ruzzante and Perry pers obs), subsequently identified as putative resident and anadromous females. Such spawning time differences have been observed among morphs in other populations (Corrigan et al. 2011; Garduno-Paz et al. 2012; Westgaard et al. 2004) but the importance of this prezygotic barrier to incipient speciation in Arctic Charr remains unknown. The ecological pressures driving this incipient speciation therefore remain largely undetermined and require further investigation.

Refugial origin may have also contributed to the incipient speciation of morphs. The introgression of multiple charr glacial lineages in Labrador (Salisbury et al. 2019) could have facilitated new genetic combinations, driving contemporary morph differentiation (Marques et al. 2019) as seen in Darwin's finches (Lamichhaney et al. 2018) and Three-spined Sticklebacks (*Gasterosteus aculeatus*) (Nelson and Cresko 2018). However, genetically distinguishable resident and anadromous charr in Svalbard and Greenland likely descend from only the Atlantic lineage (Brunner et al. 2001; Moore et al. 2015). Atlantic lineage nDNA was also evident in southeast Baffin Island charr populations that had only Arctic lineage mtDNA (Moore et al. 2015). These populations were near those with genetically undifferentiated resident and anadromous morphs (Moore et al. 2014) suggesting that Arctic and Atlantic lineage introgression here was insufficient for incipient speciation. Therefore, further investigation of the relative and

interactive importance of ecological conditions and glacial history in driving genetic differentiation is needed.

4.5.2 Caveat on Morph Identification

We note that the size differences observed among sympatric morphs are also consistent with non-anadromous small dwarf and large cannibalistic morphs, which have been found in sympatry in landlocked Charr Lake in Hebron fjord, Labrador (Bouillon and Dempson 1989). However, Ramah, Brooklyn, and Esker North Lakes are all sea-accessible (Anderson 1985; but see Van der Velden et al. 2013), unlike Charr Lake (Bouillon and Dempson 1989). While analysis based on otolith microchemistry (e.g., Radtke et al. 1997) or telemetry tagging (e.g., Moore et al. 2017) could confirm migratory behavior in the future, our results remain unaltered in suggesting limited genetic parallelism occurs between the sympatric small and big morphs identified here.

4.5.3 Parallelism vs Non-Parallelism

Most outlier SNPs were detected in a single lake suggesting a general lack of genetic parallelism among morphs. Similar observations have been made in other salmonids (e.g., Campbell and Bernatchez 2004; Feulner and Seehausen 2019; Veale and Russello 2017b). This may reflect parallel genomic regions being undetected due to drift between morphs (MacPherson and Nuisman 2017) or unsampled, despite genome-wide distribution of our SNPs. Alternatively, differing local selective pressures could drive non-parallel genetic divergence between morphs across locations, or the alternative genetic pathways could be employed in different locations to achieve the same phenotypic differentiation (Campbell and Bernatchez 2004).

For those 38 SNPs detected as outliers in more than one lake, 10 did not demonstrate parallel allelic trends. These SNPs may have been alternatively fixed due to hitchhiking if the subject of divergent selection was a nearby gene. Alternatively, this could reflect the repeated employment of the same genomic regions but in concert with different combinations of genes to alter the same biochemical pathway and achieve the same developmental consequences (Roda et al. 2013). However, only the remaining 28

SNPs detected as outliers in multiple lakes and demonstrating parallel allelic trends provide clear evidence for genetic parallelism.

A single SNP on AC32 within the gene pappalysin-2 demonstrated the strongest evidence for parallelism as it was detected as an outlier in all three lakes and demonstrated parallel allelic trends. An outlier SNP in Esker North Lake was detected in a paralog of this gene (pappalysin-2 isoform X1) located on AC19 (homeologous to AC32), further suggesting the importance of this gene to morph differentiation. Pappalysin-2 regulates Insulin-like Growth Factor in humans and is associated with stunted growth in both humans and mice (Conover et al. 2011; Dauber et al. 2016). We speculate that it might also contribute to the size dimorphism observed in our charr morphs. This potential genetic component is in contrast with the suggestion that the large size of anadromous morphs compared to resident morphs is a plastic response to the higher quality food available in the ocean (Jonsson and Jonsson 1993). Further investigation of the developmental consequences of pappalysin-2 is needed to test this hypothesis.

Two other genes demonstrating parallelism in 2/3 lakes have also been linked to morph differentiation in other salmonids. One, reticulon-4, inhibits neurite development (Magnusson et al. 2003) resulting in reduced spatial learning and memory (Zagrebelsky et al. 2017). It has been associated with both neural expression and growth rate QTL among dwarf and normal Lake Whitefish (Whiteley et al. 2008) and is differentially expressed among river and lake-dwelling Sockeye Salmon (*Oncorhynchus nerka*) (Pavey et al. 2011), Lean and Siscowet Lake Trout (*Salvelinus namaycush*) (Goetz et al. 2010), and allopatric anadromous Atlantic Salmon (*Salmo salar*) populations (Tymchuk et al. 2010). The second, spectrin beta chain non-erythrocytic 1 isoform X2 has also been found to genetically differentiate resident and migratory Brown Trout (*Salmo trutta*) (Lemopoulos et al. 2018). These results suggest that the genetic underpinnings of migratory behavior may be partially genetically conserved within salmonids.

4.5.4 Parallel Paralogs

Outlier SNPs were detected in different paralogs both within and across all lakes. Within a lake, the detection of multiple outlier paralogs suggests their importance to local

adaptation. Alternatively, the detection of different outlier paralogs in different lakes suggests their potential employment to achieve similar phenotypic differentiation among morphs. Several QTL for Arctic Charr (Norman et al. 2012) and Rainbow Trout (*Oncorhynchus mykiss*) (Nichols et al. 2008) map to homeologous chromosomes, supporting the potential conserved functionality among homeologs. Only pro-neuregulin-3, membrane-bound, had paralogs detected as outliers in all three lakes (on AC17 in Ramah, on AC25 in Brooklyn, and on AC18 in Esker North; with AC18 and AC25 being homeologous). This gene is associated with mouse neural development (Anton et al. 2004; Zhang et al. 1997) and genetically differentiates resident and migratory Brown Trout (Lemopoulos et al. 2018). Our results support the potential evolutionary importance of paralogs and homeologs to local adaptation as well as repeated morph differentiation, and incipient speciation. Alternative paralogs are known to drive convergent evolution of traits across species: e.g., red flower colouration in *Mimulus* spp. (Cooley et al. 2011) and improved sulfate transportation in sulfate-limited environments in *Saccharomyces* spp. (Sanchez et al. 2017). Yet despite the anticipated importance of paralogs to phenotypic diversity (Otto and Whitton 2000; Chen et al. 2019), paralogs are often screened out of population genomic studies prior to analyses (Limborg et al. 2016; McKinney et al. 2016) and the contribution of paralogs to repeated intra-population morph differentiation is not well-known (Conte et al. 2012; Nichols et al. 2008). Our results suggest paralogs may therefore be an important but often unobserved source of parallelism contributing to repeated incipient speciation.

4.5.5 Conclusion

We found evidence for significant genetic differentiation among sympatric, size-differentiated morphs in multiple populations in Labrador. Multiple genes differed between sympatric morphs, but those demonstrating parallelism across all lakes (i.e., pappalysin-2, pro-neuregulin-3, membrane-bound) are most likely to be key to consistently driving morph differentiation and therefore warrant future investigation of their developmental effects. However, the observed general lack of parallelism was surprising given the anticipated genetic similarity between populations. Our results add to the growing body of literature finding similarly low levels of genetic parallelism in fish

(Deagle et al. 2012; Gagnaire et al. 2013; Jacobs et al. 2020), plants (Roda et al. 2013), and invertebrates (Kess et al. 2018; Soria-Carrasco et al. 2014; Westram et al. 2014; Westram et al. 2016), suggesting a few key genes in combination with multiple alternative genetic pathways may be employed to drive repeated incipient speciation. Further investigation of the contexts in which incipient speciation is repeatable at the genomic level is therefore needed to improve our understanding of the predictability of evolution.

4.6 Data Accessibility Statement

Metadata of lake samples (including length, weight, maturity, sex) are included as Supplementary File S2. Genepop files of SNP data have been submitted to Dryad link (but will remain private until article is accepted): doi:10.5061/dryad.cz8w9gj1f (this data may be accessed by editors and reviewers using this temporary link: https://datadryad.org/stash/share/SDgeuKgVCYUZ8MmbXoa0V5U8GSGftCdN3NnLAeEUf2A).

4.7 Author Contributions

SJS and DER designed research. SJS, DER, RP, DK collected samples. SJS and GRM conducted lab work. JSL, CMN, BFK, MMF, contributed to sequencing and genotyping. DER, GRM, IRB, KKSL, TK contributed to analysis and interpretation of results. SJS analyzed data and led the writing. All authors contributed to editing the paper.

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4.9 Tables

Table 4.1 Number of morph type by lake, as determined by ADMIXTURE and boxplot results. Arctic and Atlantic lineage haplotypes from Salisbury et al. (2019). Note that the number of immature and mature, males and females do not sum to N for some lake/morph combos due to some individuals having missing morphological data. Additionally, not all individuals were haplotyped by Salisbury et al. (2019), resulting in the counts of Arctic and Atlantic lineage not summing to N for some lake/morph combos.

Lake	Morph	N	H_O	H_E	Mean (Median) Length (mm)	Immature Males	Immature Females	Mature Males	Mature Females	Atlantic Lineage	Arctic Lineage
Ramah	Big	28	0.32	0.31	387 (397)	7	6	7	8	10	5
	Small	32	0.26	0.25	130 (131)	5	7	9	10	12	6
Brooklyn	Big	16	0.24	0.22	446 (449)	5	1	9	1	0	6
	Small	42	0.34	0.33	148 (144)	9	11	8	14	0	13
Esker North	Big	21	0.30	0.30	318 (309)	8	6	6	1	9	0
	Small	33	0.30	0.31	129 (129)	6	6	9	12	12	0
	Hybrid	6	0.31	0.29	190 (192)	2	3	0	1	3	0

Table 4.2 Genes containing outlier loci differentiating sympatric morphs in two or more lakes. R stands for Ramah Lake, B for Brooklyn Lake, E for Esker North Lake. The method which identified a given SNP as an outlier is denoted: D for RDA, P for PCAdapt, F for F_{ST}.

Gene Name	Linkage Group	Protein Code	SNP Code	Relative location (bp)	Absolute location (bp)	Lakes Detected		
						R	B	E
putative Kunitz-type serine protease inhibitor isoform X2	AC04q1.29	XP_023839715.1	AX-181928867	0	17122272	F	P	
sperm-associated antigen 8	AC04q1.29	XP_023839826.1	AX-181928263	0	21046560	P,F		F
trafficking protein particle complex subunit 13 isoform X1	AC04q1.29	XP_023839957.1	AX-181931249	0	25595395		P	F
neurolysin, mitochondrial isoform X1	AC04q1.29	XP_023839960.1	AX-181931248	0	25615676		P	F
			AX-181931247	0	25615822		P	F
structural maintenance of chromosomes protein 1A	AC07	XP_023846319.1	AX-181978887	0	30696917		F	F
			AX-181936193	0	30698404		F	F
			AX-181939256	-277	30703585		F	
LOW QUALITY PROTEIN: protein FAM13B-like	AC08	XP_023848065.1	AX-181942875	0	7470428	F	P	
neutral and basic amino acid transport protein rBAT	AC08	XP_023849331.1	AX-181988503	0	46241469	F	P	
neuronal acetylcholine receptor subunit alpha-5-like	AC10	XP_023850814.1	AX-181939162	0	12661628		P,F	P,F
			AX-181939163	0	12661651		P,F	P,F
nesprin-1-like	AC14	XP_023855785.1	AX-181984809	0	8994618		P,F	F
			AX-181931124	0	8997481		P,F	
zinc finger protein 292	AC14	XP_023856562.1	AX-181940232	670	14859851	F		F
LOW QUALITY PROTEIN: ephrin-A5	AC15	XP_023859203.1	AX-181954169	0	35519615			F
			AX-182166361	0	35530218		P,F	

Table 4.2 Continued.

Gene Name	Linkage Group	Protein Code	SNP Code	Relative location (bp)	Absolute location (bp)	Lakes Detected		
						R	B	E
LOW QUALITY PROTEIN: circadian locomoter output cycles protein kaput-like	AC16	XP_023860002.1	AX-181976798	0	26547496	F		F
exocyst complex component 1 isoform X1	AC16	XP_023859950.1	AX-181986551	0	26646095	F		F
			AX-181927877	0	26655254	P,F		
ephrin-B1	AC20	XP_023866955.1	AX-181942918	0	50339858			F
			AX-181941050	0	50365371		P,F	
LOW QUALITY PROTEIN: myosin-binding protein C, slow-type-like	AC24	XP_023825267.1	AX-181943608	0	9890034	F	P	
			AX-181912912	0	9890042	F	P	
reticulon-4 isoform X1	AC25	XP_023825591.1	AX-181942621	997	21932539		P,F	
			AX-181932343	0	21939897	F	P,F	
			AX-181932342	0	21941311		P,F	
echinoderm microtubule-associated protein-like 6 isoform X1	AC25	XP_023825606.1	AX-181943178	0	21959231	P,F		
			AX-181968927	0	21981259		P,F	
spectrin beta chain, non-erythrocytic 1 isoform X2	AC25	XP_023825943.1	AX-181952420	0	22107049		P,F	
			AX-181943600	0	22129653	P,F	F	
cullin-2 isoform X3	AC27	XP_023828461.1	AX-181925879	0	24563584	F	F	
pappalysin-2	AC32	XP_023833607.1	AX-181973598	0	19625309	P,F	P	F
centrosomal protein of 126 kDa	NW_019942795.1	XP_023993346.1	AX-181931384	0	212066			F
			AX-181931385	0	212183		P	F
			AX-181931386	0	212668			F

4.10 Figures

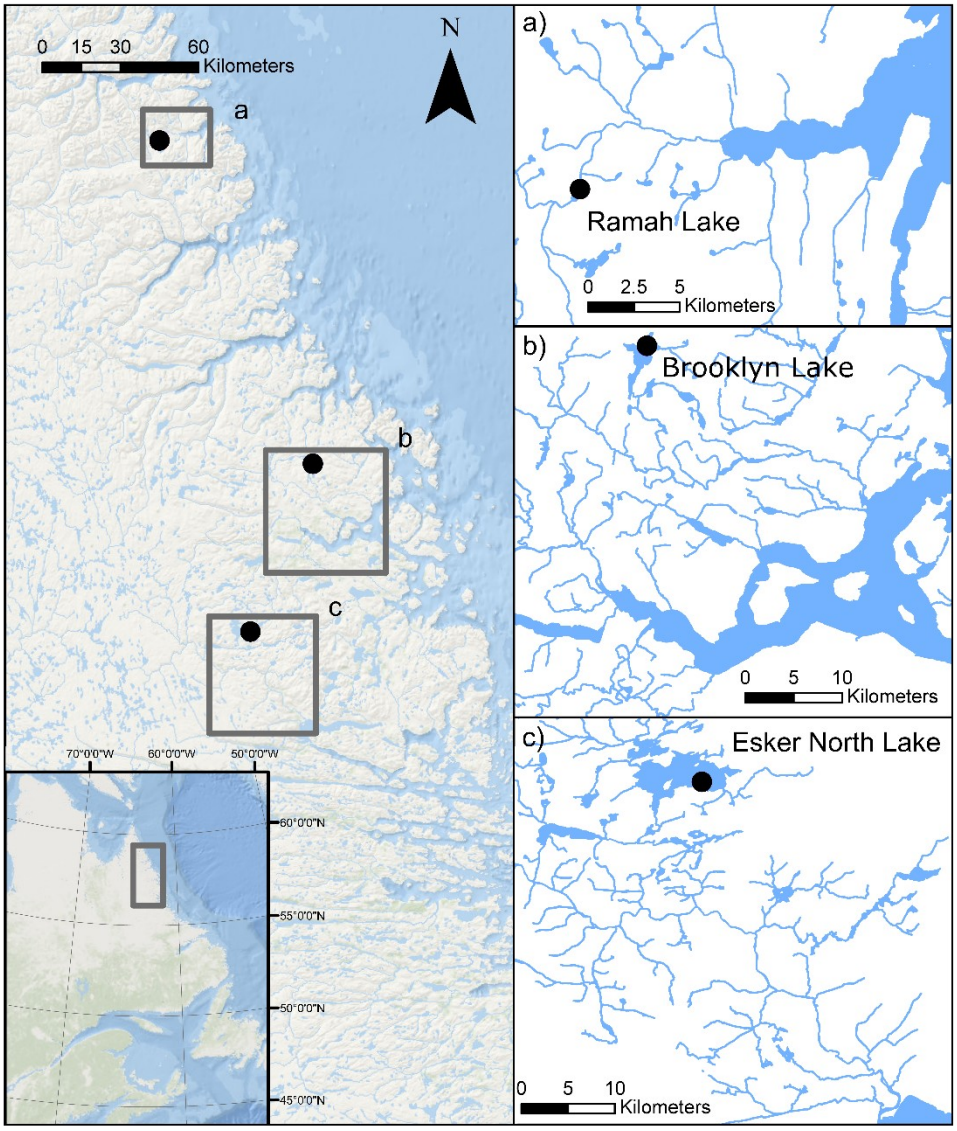
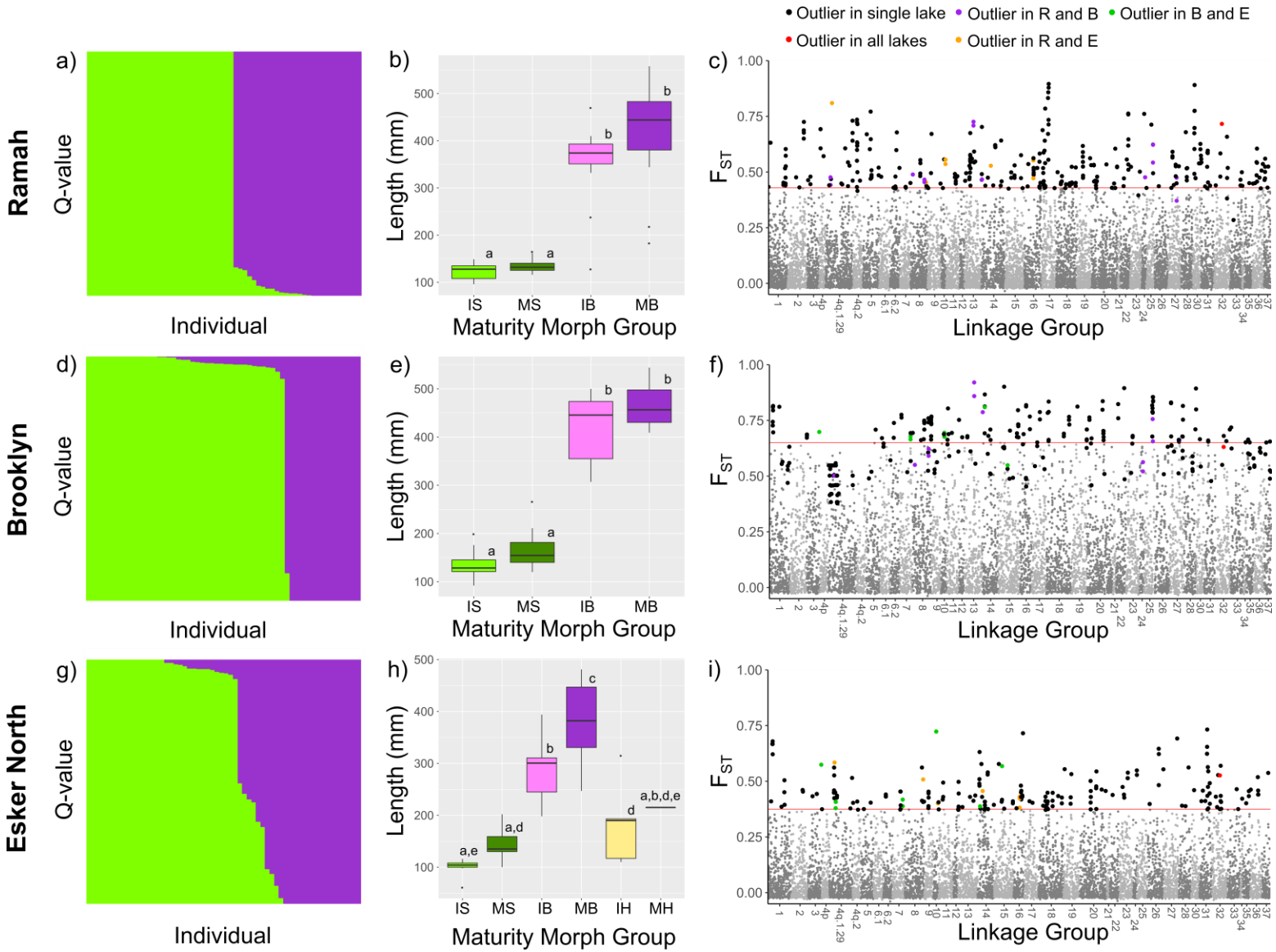


Fig.4.1 Sampling locations of Arctic Charr populations within Labrador, Canada. Black circles indicate the location of lakes containing sympatric morphs.

Fig.4.2 ADMIXTURE plots of K = 2 for a) Ramah, b) Brooklyn, c) Esker North lakes. Green bars indicate small morphs (putative residents), purple bars indicate big morphs (putative anadromous fish). Boxplots demonstrating length of fish by maturity (immature (I), mature (M)) and morph type (small (S), big (B), hybrid (H)) in d) Ramah, e) Brooklyn, and f) Esker North lakes. Shared letters among boxplots indicate alack of statistical difference after a Tukey HSD test. Manhattan plots demonstrating F_{ST} values of outlier loci detected in g) Ramah, h) Brooklyn, and i) Esker North lakes. Outlier SNPs are in bold and coloured by the lakes in which they were detected as outliers (Ramah – R, Brooklyn – B, Esker North – E), Red lines indicate 3 standard deviation above the mean F_{ST}. (Next Page)


Outlier in single lake
Outlier in R and B
Outlier in B and E
Outlier in all lakes
Outlier in R and E
Ramah
Brooklyn
Esker North
a)
b)
c)
d)
e)
f)
g)
h)
i)
Q-value
Individual
Length (mm)
Maturity Morph Group
IS
MS
IB
MB
IH
MH
F_{ST}
Linkage Group

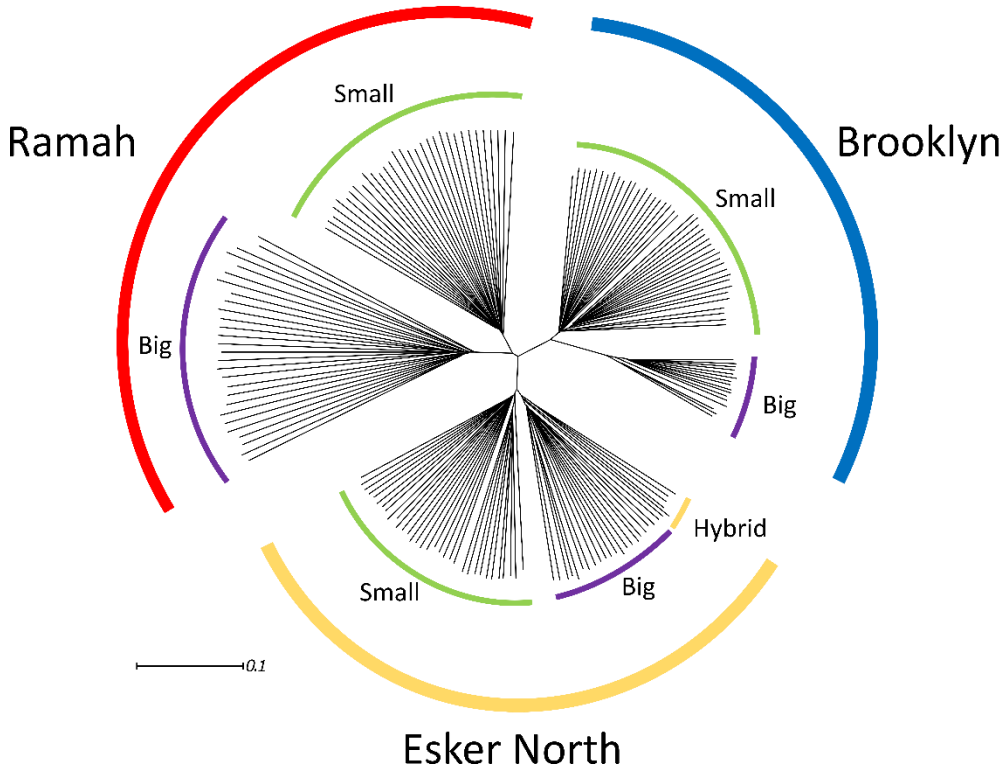


Fig.4.3 Neighbour-Joining tree of genetic distance among all samples from Ramah, Brooklyn and Esker North lakes based on N = 21404 SNPs and constructed using uncorrected (p) distances.

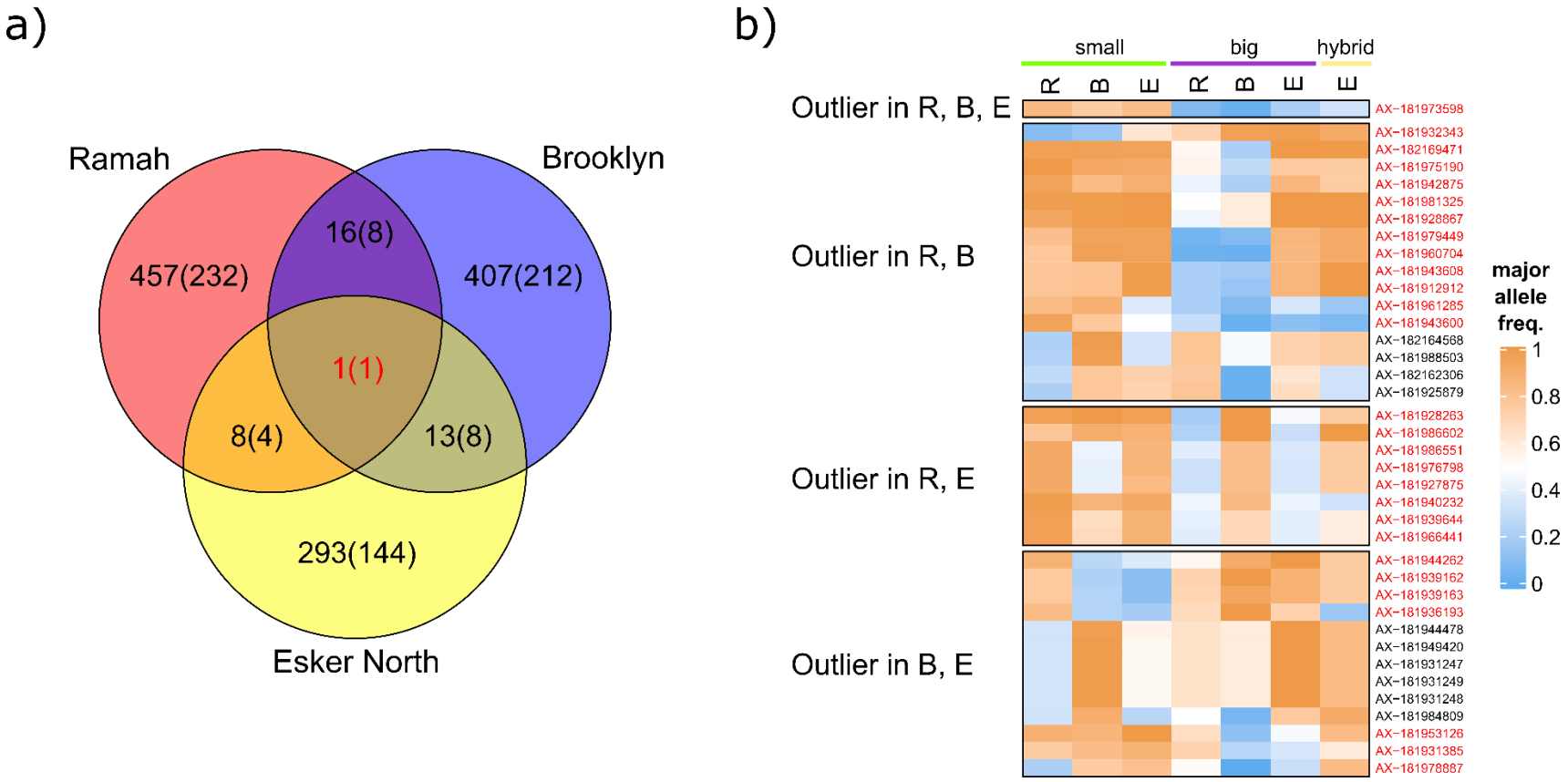


Fig.4.4 Outlier SNPs detected among sympatric Arctic Charr morphs in multiple lakes. a) Venn diagram of the number of outlier SNPs (outlier genes) detected among sympatric morphs in three lakes. Note that for those outlier genes detected in multiple lakes, different SNPs near/within that gene may have been detected as outliers for each lake. b) Heatmap of major allele frequencies of SNPs detected as outliers in two or more lakes. Loci are grouped by the lakes in which they were detected as outliers (R stands for Ramah Lake, B for Brooklyn Lake, E for Esker North Lake.). The names of loci which show parallel allelic trends across locations are highlighted in red.

4.11 Supporting Information

4.11.1 Genotyping Details

We used default sample quality control thresholds for our batch of samples: dish quality control ≥ 0.82, quality control call rate ≥ 0.97, and average call rate of passing samples on a given plate ≥ 0.985. SNP Metrics were regenerated using the "Run PS Supplemental" option as recommended (Axiom Analysis Suite User manual version 3.1) for organisms with complex genomes since some regions of the Charr genome may not have completely re-diploidized after the salmonid whole genome duplication ~ 88 mya (Macqueen and Johnston, 2014). This quality control measure may therefore help screen out putative paralogous sequence variants. Only SNPs designated as "PolyHighResolution", "NoMinorHom" and "MonoHighResolution" were included in downstream analyses. Three samples in our batch had been genotyped twice as quality control to screen out within individual non-identical SNPs. Replicate genotypes of a single individual were combined where one replicate was missing a call.

4.11.2 Additional Population Structure Analyses

We employed several population structure analyses in addition to ADMIXTURE to assessed evidence for genetic sub-structuring within each lake population. Each lake was assessed for K = 1-5 with FASTSTRUCTURE (Raj, Stephens, and Pritchard, 2014) and with the *snmf* function in the R package *LEA* (Frichot and François, 2015) using 10 repetitions. Lakes were assigned the K-value with the highest marginal likelihood using FASTSTRUCTURE and the lowest average cross-validation errors for *snmf*. Individuals within each lake were assigned to genetic groups based on Q-values for the best K-value identified for each of these two analyses. The R package *PCAdapt* (Version 4.1.0) (Luu, Bazin, and Blum, 2017) was also used to assess within-lake population structure by conducting a PCA of 20 principal components (K = 1-20) with the default Mahalanobis distance. The best K-value was assessed from the breakpoint in the screeplot of the proportion of variance associated with each principal component. Finally, population structure was assessed with a discriminant analysis of principal components (DAPC) using the R package *Adegenet* (Jombart, 2008). Samples were assigned to genetic groups within each lake using the function *find.clusters* with a max number of clusters set to 5,

all available PCs, and 10 iterations. Then a DAPC analysis was run using 1 discriminant function and 1 PC to assess the genetic relationship among these assigned groups.

Table S4.1 Sampling locations and number of samples (N) per location.

	Latitude	Longitude	Sampling Year	N	N passing QC
Ramah Lake	58.8413796	-63.477406	2014	61	60
Brooklyn Lake	57.7264811	-62.473362	2015	60	58
Esker North Lake	57.1488411	-62.878159	2015	60	60

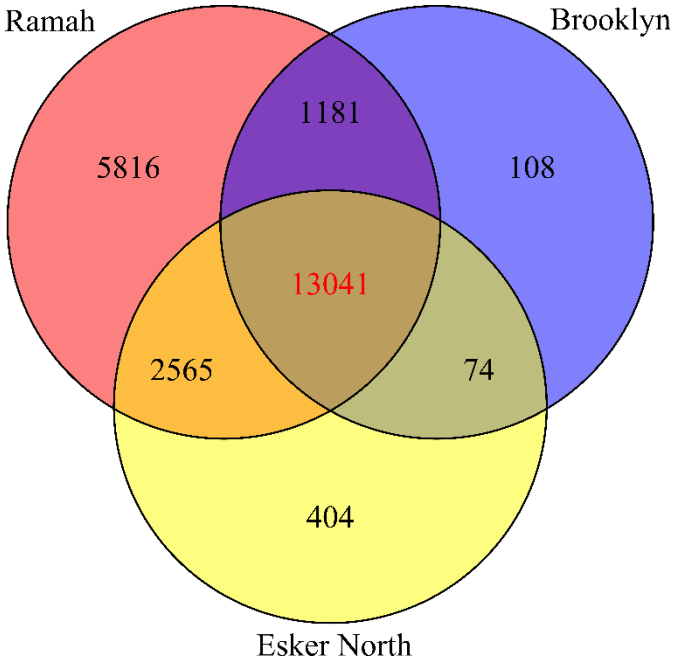


Fig.S4.1 Number of polymorphic loci detected in each lake.

4.11.3 ADMIXTURE Results

Table S4.2 Average cross-validation error estimates for ADMIXTURE results for each lake and K-value. Lowest values for each lake are shaded.

K-value	Ramah	Brooklyn	Esker North
1	0.54300	0.59381	0.57212
2	0.50676	0.52585	0.55493
3	0.53590	0.54182	0.57256
4	0.57338	0.60204	0.62099
5	0.62585	0.64725	0.66333

4.11.4 FASTSTRUCTURE Results

Table S4.3 FASTSTRUCTURE K-values which maximized marginal likelihoods and were used to explain structure in data for each lake.

	Ramah	Brooklyn	Esker North
Model complexity that maximizes marginal likelihood	2	2	2
Model components used to explain structure in data	2	2	2

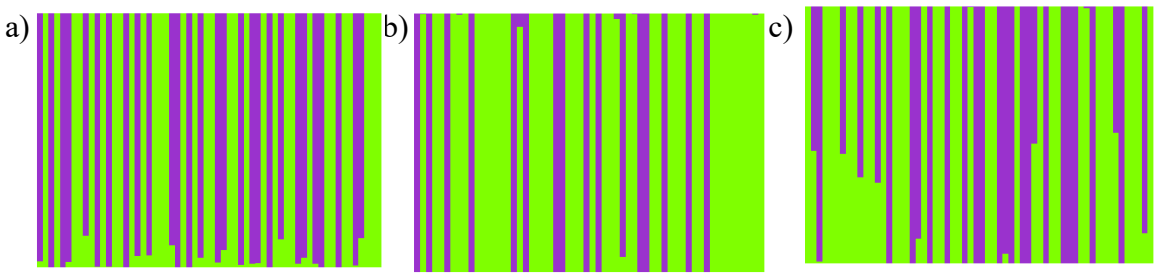


Fig.S4.2 FASTSTRUCTURE plots of K = 2 for a) Ramah, b) Brooklyn, c) Esker North lakes. Green bars indicate small (putative resident) morphs, purple bars indicate big (putative anadromous) morphs.

4.11.5 SNMF Results

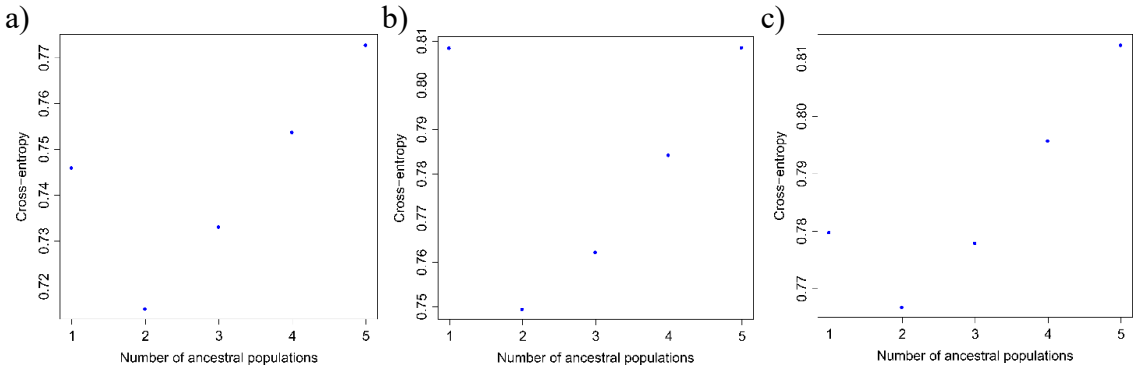


Fig.S4.3 SNMF cross-entropy values for K = 1-5 for a) Ramah, b) Brooklyn, c) Esker North lakes.

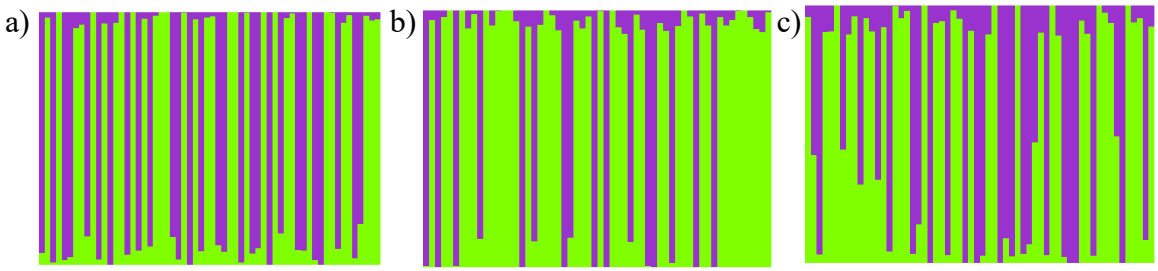


Fig.S4.4 SNMF plots of K = 2 for a) Ramah, b) Brooklyn, c) Esker North lakes. Green bars indicate small (putative resident) morphs, purple bars indicate big (putative anadromous) morphs.

4.11.6 DAPC Results

Table S4.4 BIC values for K = 1-5 using *find.clusters* function from the DAPC package for each lake. Lowest values for each lake are shaded.

K-value	Ramah	Brooklyn	Esker North
1	494.4396	459.0870	478.4383
2	490.7186	451.5936	477.2340
3	493.2215	453.6703	478.6033
4	495.8751	456.4108	480.7349
5	498.6289	459.1420	482.9955

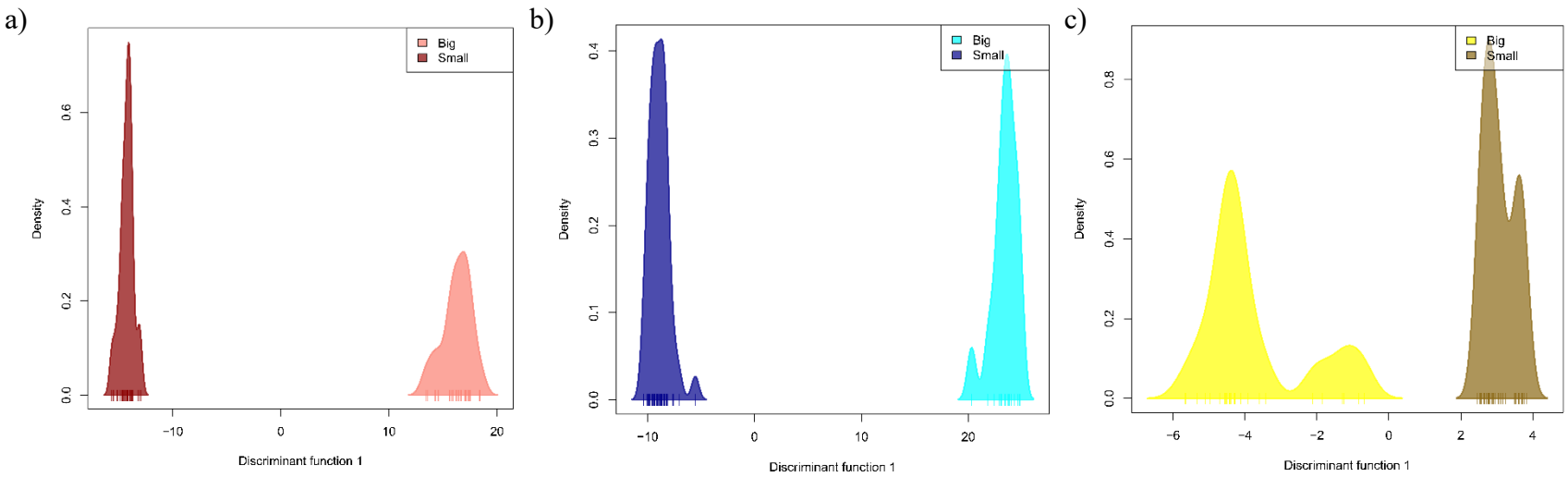


Fig.S4.5 DAPC plots of based on one discriminant function for a) Ramah, b) Brooklyn, c) Esker North lakes.

4.11.7 PCADAPT Results

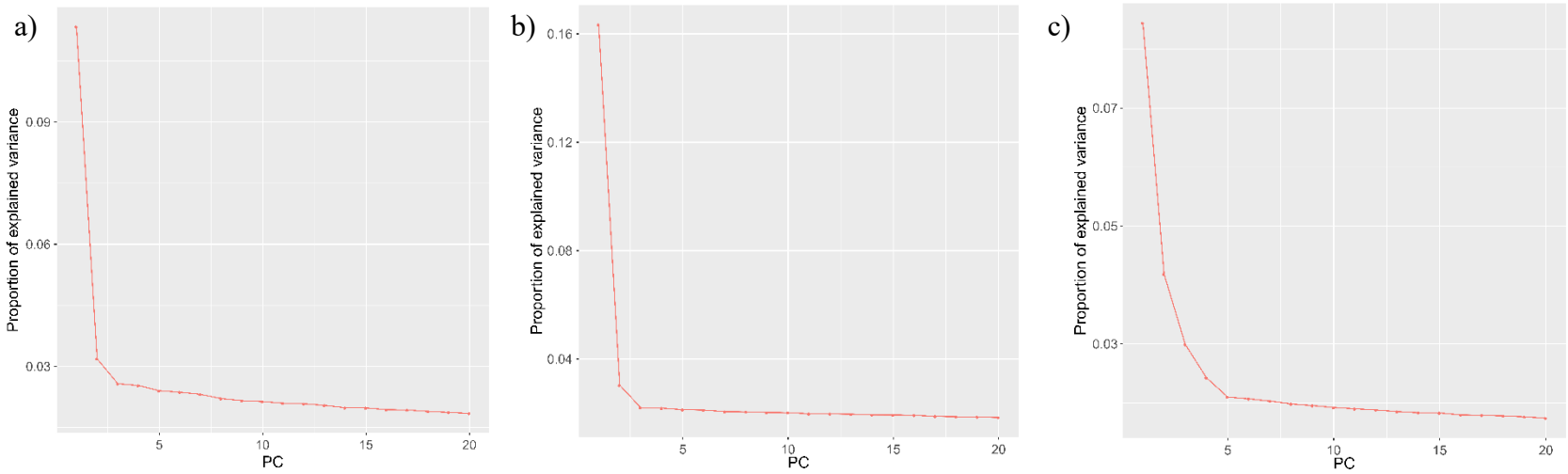


Fig.S4.6 Proportion of explained variance for each PC of PCAdapt population structure analysis for a) Ramah, b) Brooklyn, c) Esker North lakes.

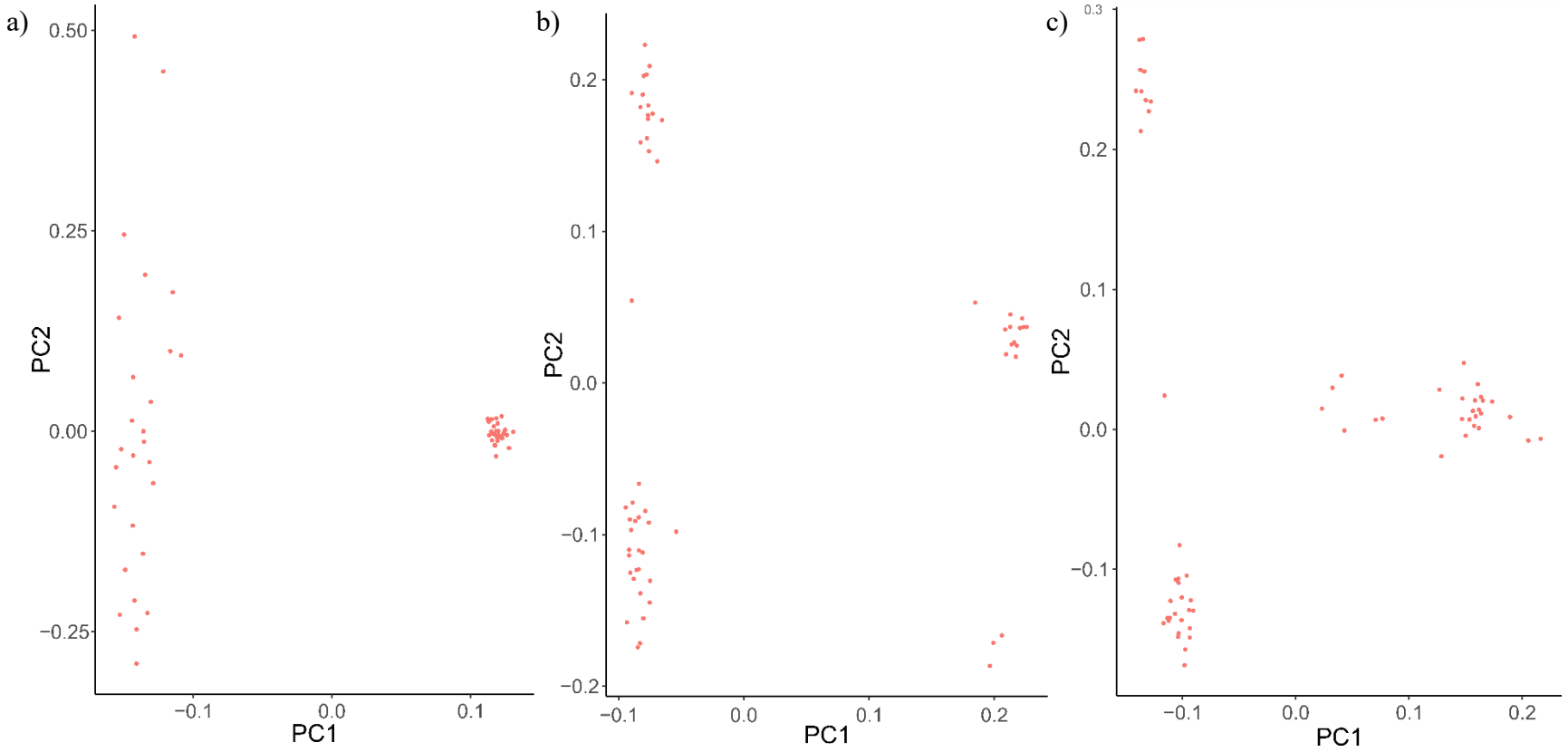


Fig.S4.7 PCAdapt population structure analysis for a) Ramah, b) Brooklyn, c) Esker North lakes.

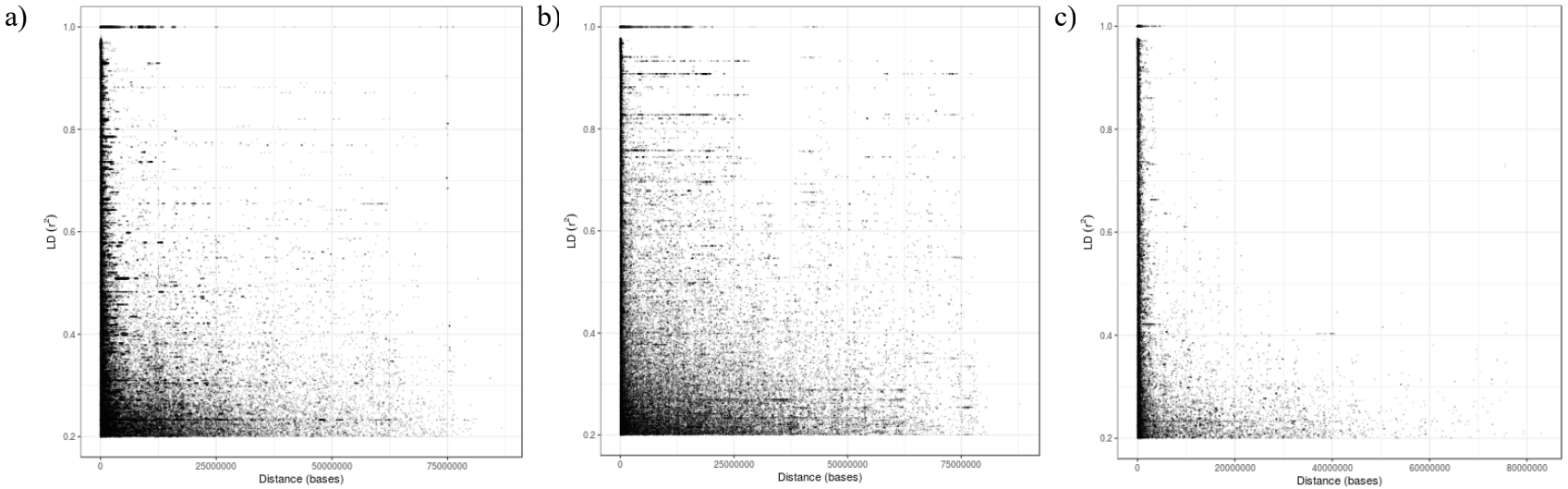


Fig.S4.8 Linkage disequilibrium decay plots for a) Ramah, b) Brooklyn, c) Esker North lakes.

4.11.8 ADMIXTURE Results Using Neutral Loci

Table S4.5 Average cross-validation error estimates for ADMIXTURE results for each lake and K-value using only neutral loci. Lowest values for each lake are shaded.

K-value	Ramah	Brooklyn	Esker North
1	0.53469	0.58607	0.56694
2	0.50673	0.52961	0.55483
3	0.53433	0.54498	0.57076
4	0.56895	0.60933	0.62445
5	0.62251	0.64761	0.66539

Fig.S4.9 ADMIXTURE plots of K = 2 for a) Ramah, b) Brooklyn, c) Esker North lakes. Green bars indicate small (putative resident) morphs, purple bars indicate big (putative anadromous) morphs.

4.11.9 Population Structure Using All Samples

Table S4.6 AMOVA results for samples from all lakes.

	Df	Sum Sq	Mean Sq	Sigma	%
Between Lakes	2	243596.1	121798.037	607.071567	9.1318061
Between Morphs Within Lake	3	134830.7	44943.561	755.690628	11.3673917
Between samples Within Morph	166	878488.1	5292.097	6.978714	0.1049765
Within samples	172	907840.0	5278.140	5278.139692	79.3958257
Total	343	2164754.9	6311.239	6647.880600	100

Table S4.7 Weighted pairwise Weir and Cockerham (1984) F_{ST} values among big and small morphs from all lakes based on 21404 SNPs.

	Brooklyn (big)	**Brooklyn (small)**	**Esker North (big)**	**Esker North (small)**	**Ramah (big)**
Brooklyn (big)	0				
Brooklyn (small)	0.20	0			
Esker North (big)	0.33	0.23	0		
Esker North (small)	0.32	0.20	0.08	0	
Ramah (big)	0.26	0.18	0.17	0.16	0
Ramah (small)	0.28	0.17	0.19	0.16	0.11

4.11.10 RDA Analysis

4.11.10.1 Ramah

Table S4.8 Significance results of full model of RDA for Ramah.

	Df	Variance	F	Pr(>F)
Model	4	2829.9	1.9321	0.001
Residual	54	19773.1		

Table S4.9 Significance results of each RDA for Ramah.

	Df	Variance	F	Pr(>F)
RDA1	1	1632.1	4.4573	0.001
RDA2	1	435.9	1.1905	0.089
RDA3	1	412.9	1.1277	0.109
RDA4	1	348.9	0.9528	0.763
Residual	54	19773.1		

Table S4.10 Significance results of each term of the RDA model for Ramah.

	Df	Variance	F	Pr(>F)
Sex	1	419.4	1.1453	0.11
Length	1	1595.9	4.3585	0.001
Weight	1	449.1	1.2264	0.05
Maturity	1	365.5	0.9982	0.341
Residual	54	19773.1		

4.11.10.2 Brooklyn

Table S4.11 Significance results of full model of RDA for Brooklyn.

	Df	Variance	F	Pr(>F)
Model	4	1934	2.0552	0.001
Residual	53	12469		

Table S4.12 Significance results of each RDA for Brooklyn.

	Df	Variance	F	Pr(>F)
RDA1	1	1173.1	4.9863	0.001
RDA2	1	353.7	1.5034	0.04
RDA3	1	224.6	0.9547	0.939
RDA4	1	182.7	0.7764	0.994
Residual	53	12469		

Table S4.13 Significance results of each term of the RDA model for Brooklyn.

	Df	Variance	F	Pr(>F)
Sex	1	701.7	2.9825	0.001
Length	1	772.8	3.2849	0.001
Weight	1	219.2	0.9318	0.606
Maturity	1	240.3	1.0215	0.31
Residual	53	12469		

4.11.10.3 Esker North

Table S4.14 Significance results of full model of RDA for Esker North.

	Df	Variance	F	Pr(>F)
Model	4	1611.4	1.5309	0.001
Residual	55	14472.6		

Table S4.15 Significance results of each RDA for Esker North.

	Df	Variance	F	Pr(>F)
RDA1	1	743.7	2.8261	0.001
RDA2	1	331.5	1.26	0.039
RDA3	1	282.1	1.0722	0.358
RDA4	1	254.1	0.9655	0.702
Residual	55	14472.6		

Table S4.16 Significance results of each term of the RDA model for Esker North.

	Df	Variance	F	Pr(>F)
Sex	1	292.9	1.1131	0.109
Length	1	609.7	2.317	0.001
Weight	1	378.5	1.4384	0.005
Maturity	1	330.3	1.2552	0.03
Residual	55	14472.6		

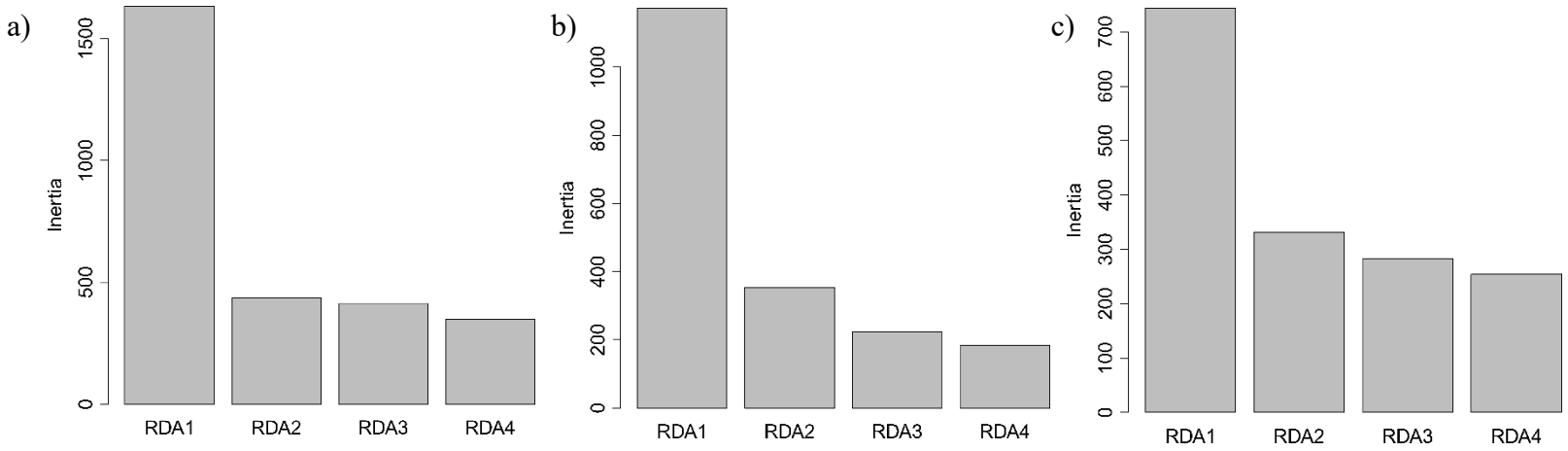


Fig.S4.10 Inertias of RDAs 1-4 for a) Ramah, b) Brooklyn, c) Esker North lakes.

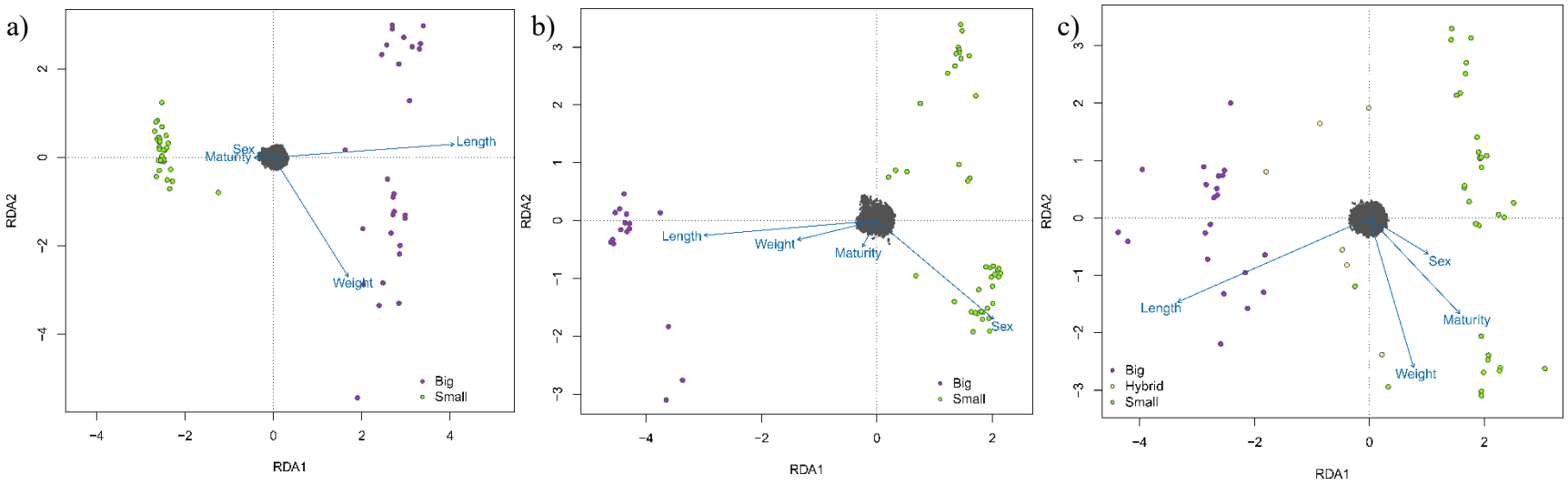


Fig.S4.11 RDA plots of genomic versus morphological data (length, weight, maturity, sex) for a) Ramah, b) Brooklyn, c) Esker North lakes.

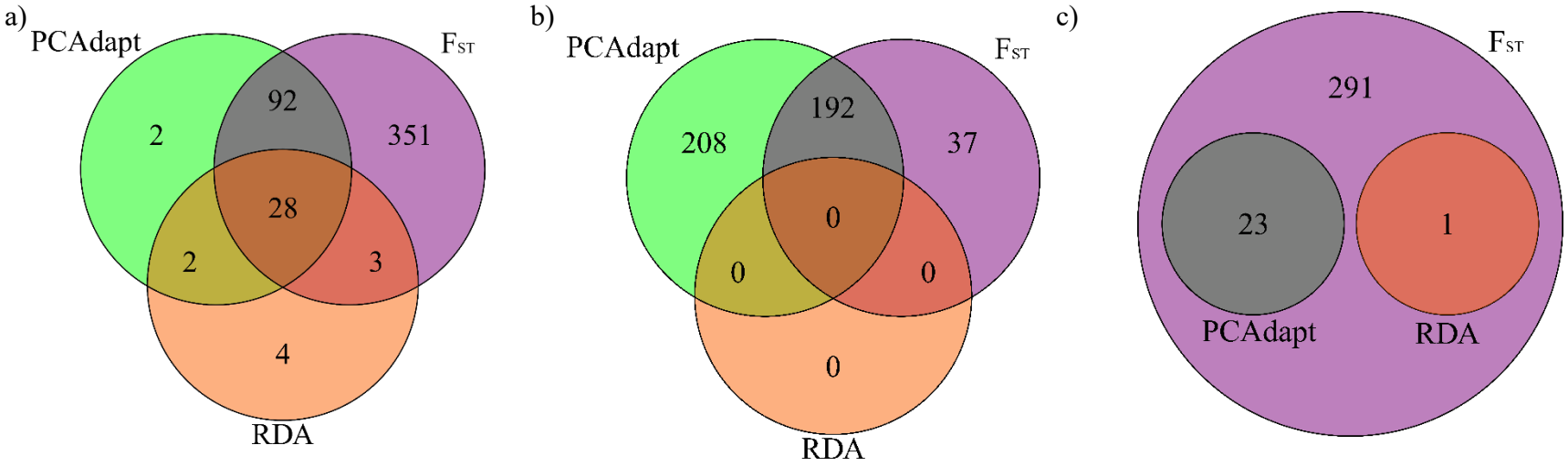


Fig.S4.12 Number of loci detected as an outlier in each of a) Ramah, b) Brooklyn, c) Esker North lakes, by outlier detection method (PCAdapt, F_{ST}, RDA).

Table S4.17 The number of outlier and non-outlier SNPs detected between morphs within a given lake found to be polymorphic outliers, polymorphic non-outliers or non-polymorphic in each of the three lakes.

	Ramah (N = 22603)		Brooklyn (N = 14404)		Esker North (N = 16084)	
	Outlier (N = 482)	Non-outlier (N = 22121)	Outlier (N = 437)	Non-outlier (N = 13967)	Outlier (N = 315)	Non-outlier (N = 15769)
Ramah Polymorphic Outlier	482	0	17	371	9	393
Ramah Polymorphic Non-outlier	0	22121	400	13434	299	14905
Ramah Non-polymorphic	0	0	20	162	7	471
Brooklyn Polymorphic Outlier	17	400	437	0	14	347
Brooklyn Polymorphic Non-outlier	371	13434	0	13967	272	12482
Brooklyn Non-polymorphic	94	8287	0	0	29	2940
Esker North Polymorphic Outlier	9	299	14	272	315	0
Esker North Polymorphic Non-outlier	393	14905	347	12482	0	15769
Esker North Non-polymorphic	80	6917	76	1213	0	0

Table S4.18 Top Biological Processes GO terms with an unadjusted p-value < 0.01 for outlier loci detected by all methods in any lake.

GO.ID	Term	Annotated	Significant	Expected	weight01	weight01padj
GO:0006294	nucleotide-excision repair, preincision ...	6	4	0.37	0.0002	1
GO:0071479	cellular response to ionizing radiation	69	11	4.3	0.00037	1
GO:0000717	nucleotide-excision repair, DNA duplex u...	4	3	0.25	0.00092	1
GO:0010873	positive regulation of cholesterol ester...	4	3	0.25	0.00092	1
GO:0018343	protein farnesylation	4	3	0.25	0.00092	1
GO:0034394	protein localization to cell surface	101	10	6.3	0.00095	1
GO:0051775	response to redox state	14	5	0.87	0.00146	1
GO:0070213	protein auto-ADP-ribosylation	5	3	0.31	0.00219	1
GO:0071245	cellular response to carbon monoxide	5	3	0.31	0.00219	1
GO:0090503	RNA phosphodiester bond hydrolysis, exon...	16	5	1	0.00228	1
GO:0010812	negative regulation of cell-substrate ad...	99	12	6.17	0.00229	1
GO:0060135	maternal process involved in female preg...	64	11	3.99	0.00287	1
GO:0030509	BMP signaling pathway	182	17	11.35	0.00387	1
GO:0018992	germ-line sex determination	9	3	0.56	0.00388	1
GO:0042415	norepinephrine metabolic process	10	3	0.62	0.00388	1
GO:0000962	positive regulation of mitochondrial RNA...	2	2	0.12	0.00388	1
GO:0006211	5-methylcytosine catabolic process	2	2	0.12	0.00388	1
GO:0035511	oxidative DNA demethylation	2	2	0.12	0.00388	1
GO:0035928	rRNA import into mitochondrion	2	2	0.12	0.00388	1
GO:0090364	regulation of proteasome assembly	2	2	0.12	0.00388	1
GO:0097222	mitochondrial mRNA polyadenylation	2	2	0.12	0.00388	1
GO:1903928	cellular response to cyanide	2	2	0.12	0.00388	1
GO:1904743	negative regulation of telomeric DNA bin...	2	2	0.12	0.00388	1
GO:0001936	regulation of endothelial cell prolifera...	130	14	8.11	0.00412	1
GO:0003342	proepicardium development	6	3	0.37	0.00419	1

Table S4.18 Continued.

GO.ID	Term	Annotated	Significant	Expected	weight01	weight01padj
GO:2001045	negative regulation of integrin-mediated...	6	3	0.37	0.00419	1
GO:0035640	exploration behavior	60	9	3.74	0.00448	1
GO:0006089	lactate metabolic process	15	4	0.94	0.00697	1
GO:0010870	positive regulation of receptor biosynth...	7	3	0.44	0.00699	1
GO:2000627	positive regulation of miRNA catabolic p...	7	3	0.44	0.00699	1
GO:0014850	response to muscle activity	47	8	2.93	0.0079	1
GO:0003222	ventricular trabecula myocardium morphog...	21	5	1.31	0.00818	1
GO:0045906	negative regulation of vasoconstriction	19	5	1.18	0.00903	1
GO:0018105	peptidyl-serine phosphorylation	329	28	20.52	0.00908	1
GO:1990869	cellular response to chemokine	42	5	2.62	0.00911	1
GO:0034332	adherens junction organization	250	30	15.59	0.00923	1
GO:0001974	blood vessel remodeling	90	12	5.61	0.00949	1
GO:0045648	positive regulation of erythrocyte diffe...	39	7	2.43	0.00949	1

Table S4.19 Top Biological Processes GO terms with an unadjusted p-value < 0.01 for outlier loci detected in two or more lakes.

GO.ID	Term	Annotated	Significant	Expected	weight01	weight01padj
GO:0007182	common-partner SMAD protein phosphorylat...	4	2	0.01	4.70E-05	0.71487
GO:0015811	L-cystine transport	1	1	0	0.0029	1
GO:0071361	cellular response to ethanol	29	2	0.08	0.003	1
GO:0031286	negative regulation of sorocarp stalk ce...	2	1	0.01	0.0057	1
GO:0036369	transcription factor catabolic process	2	1	0.01	0.0057	1
GO:0051759	sister chromosome movement towards spind...	2	1	0.01	0.0057	1
GO:0007052	mitotic spindle organization	109	3	0.31	0.0063	1
GO:0007274	neuromuscular synaptic transmission	45	2	0.13	0.0072	1
GO:0065007	biological regulation	6256	19	17.91	0.0075	1
GO:0016198	axon choice point recognition	28	2	0.08	0.0082	1
GO:0019100	male germ-line sex determination	3	1	0.01	0.0086	1
GO:0048694	positive regulation of collateral sprout...	3	1	0.01	0.0086	1
GO:0051232	meiotic spindle elongation	3	1	0.01	0.0086	1
GO:1902104	positive regulation of metaphase/anaphas...	3	1	0.01	0.0086	1
GO:1905580	positive regulation of ERBB3 signaling p...	3	1	0.01	0.0086	1
GO:1905943	negative regulation of formation of grow...	3	1	0.01	0.0086	1

Table S4.20 Paralogous genes containing outlier loci differentiating sympatric morphs in the same lake population. R stands for Ramah Lake, B for Brooklyn Lake, E for Esker North Lake. For a given gene, starred linkage groups are homeologous. Please note that multiple SNPs may have identified as outliers within a given gene.

Lake	General Gene Name	Linkage Group	Protein Code	Specific Gene Name	SNP Code	Relative location (bp)	Absolute location (bp)
R	IgGFc-binding protein	AC30	XP_023831364.1	IgGFc-binding protein	AX-181930173	0	26014267
		AC32	XP_023833881.1	LOW QUALITY PROTEIN: IgGFc-binding protein-like	AX-181986439	0	15900714
		AC32	XP_023833881.1	LOW QUALITY PROTEIN: IgGFc-binding protein-like	AX-181932036	0	15902215
R	neurabin-2	AC20	XP_023868571.1	neurabin-2-like	AX-182160962	0	10127550
		AC20	XP_023868571.1	neurabin-2-like	AX-182160344	0	10127798
		AC20	XP_023867184.1	neurabin-2	AX-181939786	0	10462360
B	erbin	AC04q1.29 *	XP_023839965.1	erbin isoform X1	AX-181949419	0	25701933
		AC04q1.29 *	XP_023839965.1	erbin isoform X1	AX-181978827	0	25713376
		AC05 *	XP_023843303.1	erbin isoform X3	AX-181944578	0	12994813
B	leucine-rich repeat transmembrane neuronal protein 4	AC04q1.29	XP_023839661.1	leucine-rich repeat transmembrane neuronal protein 4-like	AX-181932423	0	14729515
		AC04q1.29	XP_023839672.1	leucine-rich repeat transmembrane neuronal protein 4-like isoform X1	AX-181928857	0	15757635

Table S4.20 Continued.

Lake	General Gene Name	Linkage Group	Protein Code	Specific Gene Name	SNP Code	Relative location (bp)	Absolute location (bp)
B	MAM domain-containing glycosylphosphatidylinositol anchor protein 2	AC28	XP_023829394.1	MAM domain-containing glycosylphosphatidylinositol anchor protein 2-like	AX-181939692	0	25461935
		AC28	XP_023829395.1	MAM domain-containing glycosylphosphatidylinositol anchor protein 2-like	AX-181975574	0	25612866
		AC28	XP_023829395.1	MAM domain-containing glycosylphosphatidylinositol anchor protein 2-like	AX-181941688	0	25669073
		AC28	XP_023829395.1	MAM domain-containing glycosylphosphatidylinositol anchor protein 2-like	AX-181962642	0	25677115
B	multidrug resistance-associated protein 4	AC27	XP_023828822.1	multidrug resistance-associated protein 4	AX-182163281	0	37024139
		AC27	XP_023828808.1	multidrug resistance-associated protein 4-like	AX-181990224	0	37033573
B	tankyrase-1	AC04q1.29	XP_023839375.1	tankyrase-1 isoform X1	AX-181962239	0	9075959
		AC15	XP_023857971.1	tankyrase-1 isoform X4	AX-181915612	0	28697847
B	transmembrane protein 184B	AC18	XP_023864770.1	transmembrane protein 184B	AX-181980049	0	62947645
		AC20	XP_023868046.1	transmembrane protein 184B isoform X1	AX-182164598	0	2743673
B	voltage-dependent N-type calcium channel subunit alpha-1B	AC04q1.29	XP_023839938.1	voltage-dependent N-type calcium channel subunit alpha-1B-like isoform X2	AX-181966589	0	24355531
		NW_019951012.1	XP_024001415.1	voltage-dependent N-type calcium channel subunit alpha-1B-like	AX-181947302	1248	1127

Table S4.20 Continued.

Lake	General Gene Name	Linkage Group	Protein Code	Specific Gene Name	SNP Code	Relative location (bp)	Absolute location (bp)
E	desmoglein-2	AC16	XP_023859541.1	desmoglein-2	AX-181989944	0	31303194
		AC16	XP_024003333.1	desmoglein-2 isoform X2	AX-181927197	0	31350042
		AC16	XP_024003333.1	desmoglein-2 isoform X2	AX-181927196	0	31353286
E	pappalysin-2	AC19 *	XP_023866013.1	pappalysin-2 isoform X1	AX-181914229	0	22485187
		AC32 *	XP_023833607.1	pappalysin-2	AX-181973598	0	19625309

Table S4.21 Genes for which different paralogous outlier loci were detected in different lake populations. R stands for Ramah Lake, B for Brooklyn Lake, E for Esker North Lake. For a given gene, starred linkage groups are homeologous.

General Gene Name	Linkage Group	Protein Code	Specific Gene Name	SNP Code	Relative location (bp)	Absolute location (bp)	Lake
cadherin-12	AC19	XP_023864956.1	cadherin-12	AX-181974510	0	20455681	E
	AC27	XP_023829039.1	cadherin-12-like	AX-181946053	0	22361919	B
catenin alpha-2	NW_019942623.1	XP_023992016.1	catenin alpha-2-like	AX-181972837	0	383287	B
	NW_019957574.1	XP_024002267.1	LOW QUALITY PROTEIN: catenin alpha-2-like	AX-181941708	0	108640	R
	NW_019957574.1	XP_024002267.1	LOW QUALITY PROTEIN: catenin alpha-2-like	AX-181941709	0	108668	R
	NW_019957574.1	XP_024002267.1	LOW QUALITY PROTEIN: catenin alpha-2-like	AX-182166741	0	148927	R
discoidin, CUB and LCCL domain-containing protein 1	AC28	XP_023829784.1	discoidin, CUB and LCCL domain-containing protein 1-like	AX-181960755	0	12803140	R
	AC35	XP_023836429.1	discoidin, CUB and LCCL domain-containing protein 1	AX-181939792	0	19930698	E
leucine-rich repeat transmembrane neuronal protein 4	AC04q1.29 *	XP_023839661.1	leucine-rich repeat transmembrane neuronal protein 4-like	AX-181932423	0	14729515	B
	AC04q1.29 *	XP_023839672.1	leucine-rich repeat transmembrane neuronal protein 4-like isoform X1	AX-181928857	0	15757635	B
	AC05 *	XP_023843574.1	leucine-rich repeat transmembrane neuronal protein 4-like	AX-181943854	0	24615926	R
opsin-5	AC16	XP_023859543.1	opsin-5-like	AX-181944047	4687	31430031	E
	AC17	XP_023861129.1	opsin-5-like	AX-181972643	0	5042735	R
PAN2-PAN3 deadenylation complex catalytic subunit PAN2	AC07 *	XP_023847330.1	PAN2-PAN3 deadenylation complex catalytic subunit PAN2	AX-181977426	0	25038612	E
	AC07 *	XP_023847330.1	PAN2-PAN3 deadenylation complex catalytic subunit PAN2	AX-181935260	0	25047954	E
	AC17 *	XP_023861482.1	PAN2-PAN3 deadenylation complex catalytic subunit PAN2 isoform X1	AX-181952107	-2559	22685483	R

Table S4.21 Continued.

General Gene Name	Linkage Group	Protein Code	Specific Gene Name	SNP Code	Relative location (bp)	Absolute location (bp)	Lake
pappalysin-2	AC19 *	XP_023866013.1	pappalysin-2 isoform X1	AX-181914229	0	22485187	E
	AC32 *	XP_023833607.1	pappalysin-2	AX-181973598	0	19625309	B
	AC32 *	XP_023833607.1	pappalysin-2	AX-181973598	0	19625309	E
	AC32 *	XP_023833607.1	pappalysin-2	AX-181973598	0	19625309	R
polyribonucleotide nucleotidyltransferase 1, mitochondrial	AC18 *	XP_023863859.1	polyribonucleotide nucleotidyltransferase 1, mitochondrial	AX-181925679	0	45537202	R
	AC25 *	XP_023826143.1	polyribonucleotide nucleotidyltransferase 1, mitochondrial isoform X1	AX-181935603	0	21796247	B
	AC25 *	XP_023826143.1	polyribonucleotide nucleotidyltransferase 1, mitochondrial isoform X1	AX-181981186	0	21798000	B
pro-neuregulin-3, membrane-bound	AC17	XP_023860894.1	pro-neuregulin-3, membrane-bound isoform-like	AX-181941701	0	38644082	R
	AC18 *	XP_023864068.1	pro-neuregulin-3, membrane-bound isoform	AX-181942151	0	21541076	E
	AC25 *	XP_023825564.1	pro-neuregulin-3, membrane-bound isoform isoform X2	AX-181942348	0	20692272	B
protein diaphanous homolog 2	AC06.2 *	XP_023846047.1	LOW QUALITY PROTEIN: protein diaphanous homolog 2-like	AX-181974082	0	16312118	R
	AC08 *	XP_023848587.1	LOW QUALITY PROTEIN: protein diaphanous homolog 2-like	AX-181946223	0	25150328	B
receptor-type tyrosine-protein phosphatase U	AC30	XP_023990454.1	LOW QUALITY PROTEIN: receptor-type tyrosine-protein phosphatase U	AX-181942714	0	10297370	R
	NW_019943148.1	XP_023995107.1	receptor-type tyrosine-protein phosphatase U-like	AX-181987996	0	137217	E

Table S4.21 Continued.

General Gene Name	Linkage Group	Protein Code	Specific Gene Name	SNP Code	Relative location (bp)	Absolute location (bp)	Lake
ryanodine receptor 3	AC09	XP_024003037.1	LOW QUALITY PROTEIN: ryanodine receptor 3-like	AX-181987612	0	19288028	E
	NW_019957557.1	XP_024002120.1	ryanodine receptor 3-like	AX-181965989	0	48984	R
serine/threonine-protein kinase tousled	AC18	XP_023863686.1	serine/threonine-protein kinase tousled-like 2 isoform X2	AX-181956617	0	16069930	R
	NW_019942545.1	XP_023991122.1	serine/threonine-protein kinase tousled-like 2 isoform X1	AX-181980625	-2791	326354	B
UV excision repair protein RAD23 homolog B	AC16	XP_023859297.1	UV excision repair protein RAD23 homolog B	AX-181989001	0	11191659	E
	AC20	XP_023867653.1	UV excision repair protein RAD23 homolog B isoform X2	AX-181930123	0	65506409	R
zinc-binding protein A33	AC03	XP_023869621.1	zinc-binding protein A33-like	AX-181985326	0	1932008	B
	AC04q1.29	XP_023839578.1	zinc-binding protein A33 isoform X1	AX-181936754	0	13344761	R
zinc transporter 6	AC18 *	XP_023863635.1	zinc transporter 6 isoform X1	AX-181925681	0	46091590	R
	AC25 *	XP_023825881.1	zinc transporter 6 isoform X1	AX-181952417	1982	22295805	B

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CHAPTER 5 - THE LOSS OF ANADROMY IN AN ARCTIC FISH (*SALVELINUS ALPINUS*): GENETIC CAUSES, CONSEQUENCES, AND CONSISTENCY

5.1 Abstract

The potentially significant genetic consequences associated with the loss of migratory capacity of diadromous fishes which have become "landlocked" in fresh water are poorly understood. Consistent selective pressures associated with freshwater residency may drive repeated differentiation both within landlocked populations (resulting in sympatric morphs) and between allopatric landlocked and anadromous populations. Alternatively, the strong genetic drift anticipated in isolated landlocked populations could hinder consistent adaptation and restrict genetic parallelism. Understanding the degree of genetic parallelism underlying differentiation has implications for both the predictability of evolution and management practices. We employed an 87k SNP array to examine the genetic characteristics of landlocked and anadromous Arctic Charr (*Salvelinus alpinus*) populations from five drainages within Labrador, Canada. Landlocked populations were highly genetically distinguishable in comparison to anadromous populations. Two landlocked populations demonstrated genetic sub-structuring but only a single outlier gene between sympatric genetic groups was detected in both populations. Most outlier SNPs detected between landlocked and anadromous populations paired by drainage were also inconsistent across pairs, potentially due to drift. However, several SNPs, genes, and paralogs, were consistently detected as outliers between multiple pairs of landlocked and anadromous populations, suggesting genetic parallelism. Our results indicate that despite their isolation, selection may drive genetically consistent incipient speciation and local adaptation in landlocked populations.

5.2 Introduction

The loss of migratory capacity is a fundamental promoter of neutral and adaptive differentiation (Waters et al. 2020). Such a loss is frequently observed in diadromous fishes, whose "landlocking" in post-glacial lakes offers a unique opportunity to study the predictability of evolution (Elmer and Meyer 2011; Delgado et al. 2020). These populations were formed subsequent to the last glacial maximum (< 20000 years) when

anadromous individuals became trapped in fresh water environments (typically lakes) through a variety of both natural and anthropogenic mechanisms including isostatic rebound and the construction of impoundments (Lee and Bell 1999). Once landlocked, fish maintain a freshwater resident life history and these populations typically exchange minimal to no gene flow with other populations (e.g., Hindar et al. 1991; Palkovacs et al. 2008; Delgado et al. 2019). The isolation of recently landlocked populations makes them ideal natural replicates of evolution (Lee and Bell 1999; Delgado et al. 2020) that may be compared to assess the predictability of their genetic differentiation.

Consistent selective pressures could drive repeated differentiation both within and across landlocked populations (Elmer et al. 2014; Jacobs et al. 2020; McGee et al. 2020). Landlocked populations are effectively released from selective pressures associated with saltwater environments resulting in predictable physiological changes in osmoregulation (Velotta et al. 2014) and swimming capacity (Velotta et al. 2018). Other consistent environmental differences between landlocked and diadromous populations include: predation (Hendry et al. 2004), prey composition (Palkovacs et al. 2008), parasites (Bouillon and Dempson 1989), and fishing effort (Hendry et al. 2004). The significant selective pressures expected to reliably differ between landlocked and diadromous fish populations could result in consistent genetic differentiation as was observed in freshwater populations of Three-spined Stickleback (*Gasterosteus aculeatus*) which repeatedly employ consistent adaptive genetic pathways either from standing genetic (Nelson and Cresko 2018) or through repeated mutations of similar genomic regions (Xie et al. 2019). However, the degree of genomic parallelism that underlies the allopatric differentiation of landlocked and diadromous fishes more broadly remains largely unknown (Delgado et al. 2019, 2020; Kjærner-Semb et al. 2020). Within landlocked populations, rapid radiations driven by ecological speciation (Schluter and Nagel 1995; Schluter 1996b) and resulting in phenotypically differentiated morphs are frequently observed (Lee and Bell 1999; Schultz and McCormick 2012). However, few studies have investigated the degree to which this repeated phenotypic differentiation is driven by consistent adaptive genetic differentiation (but see Veale and Russello 2017b; Jacobs et al. 2020; Delgado et al. 2020). Genetic drift is a potentially major impediment to genetic parallelism in landlocked populations which could be facilitated by a lack of gene flow

(Bernatchez et al. 2002) or by limited genetic diversity due to reduced carrying capacities in landlocked lakes (McCracken et al. 2013), or founder effects (Ramstad et al. 2004). We were interested in examining the degree of consistency in adaptive differentiation both within landlocked and between landlocked and anadromous populations.

Labrador, Canada is an ideal location to conduct such work as it contains numerous landlocked populations of Arctic Charr that occur in the same drainage as contemporarily anadromous populations (Anderson 1985) thus forming natural paired replicates of allopatric differentiation. These landlocked populations were formed relatively recently as Labrador was covered by ice up until 9000 years BP (Bryson et al. 1969; Occhietti et al. 2011). As in other areas of Canada, anadromous populations are fished in Labrador as part of economically and culturally important subsistence, recreational, and commercial fisheries (Andrews and Lear 1956; Scott and Crossman 1973; Dempson et al. 2008). There has been little study of the genetic structure of landlocked charr populations within Labrador in contrast to anadromous populations (e.g., Bernatchez et al. 1998; Layton et al. 2020). We previously found lower genetic diversity in landlocked than in anadromous populations using microsatellites (Salisbury et al. 2018) and mtDNA (Salisbury et al. 2019). Though neutral genetic differentiation between landlocked and anadromous Arctic Charr populations has previously been assessed (Bernatchez et al. 1998; Kapralova et al. 2011; Salisbury et al. 2018), adaptive genetic differences between landlocked and anadromous populations remain uncharacterized in this species.

Genetically distinguishable sympatric morphs of Arctic Charr have been previously identified in two landlocked lakes in Labrador using neutral microsatellites (Salisbury et al. 2018), suggesting evidence for incipient speciation. Size-differentiated, genetically distinguishable ecotypes of Arctic Charr have been observed within nearby lakes in Newfoundland (Gomez-Uchida et al. 2008) and northern Quebec (Power et al. 2009). However, the prevalence of such incipient speciation within Labrador landlocked lakes as well as the repeatability of the adaptive genetic differentiation associated with such sympatric morphs across populations remains unknown. Our recent work in this region has revealed limited genetic parallelism across sea-accessible populations containing size-differentiated sympatric morphs (consistent with putative resident and

anadromous morphs) (Salisbury et al. 2020). The overlap in the genetic mechanisms driving incipient speciation within sea-accessible and within landlocked populations of Arctic Charr remain unexplored. Little genetic parallelism has also been observed between ecologically-differentiated sympatric morphs across Scottish and Russian landlocked populations (Jacobs et al. 2020). However, unlike Scottish and Russian landlocked charr populations which were founded solely by the Atlantic and Siberian lineages respectively (Moore et al. 2015), Labrador landlocked populations demonstrate mtDNA haplotypes consistent with Acadian, Atlantic, and Arctic glacial lineages (Salisbury et al. 2019). The likely introgression between these lineages prior to establishment of landlocked populations could have increased genetic diversity and facilitated many genetic pathways to achieve similar morphological differentiation. Alternatively, such high historic gene flow could have homogenized the genetic variation among populations, allowing for the use of identical genetic pathways to achieve similar morphological differentiation. The effects of this unique colonization history of Labrador on the genetic repeatability of incipient speciation in landlocked populations is therefore unknown.

Insight into the character and consistency of the adaptive genetic differentiation between sympatric morphs within landlocked populations and between allopatric landlocked and anadromous populations has significant consequences both for our understanding of the predictability of evolution and for the management of sympatric and allopatric populations. We employed a newly-designed 87k SNP array (Nugent et al. 2019) to characterize the adaptive differentiation and examine evidence of incipient speciation between sympatric morphs within landlocked populations and between paired landlocked and anadromous populations from the same drainage area. We then assessed for evidence of genetic parallelism both across replicate landlocked populations with sympatric genetically distinguishable morphs and across replicate pairs of allopatric landlocked and anadromous populations. Given the recent whole genome duplication in salmonids (Macqueen and Johnston 2014), we examined whether different landlocked populations were employing different paralogs of the same gene to drive either incipient speciation or adaptive differentiation from anadromous populations. We therefore assessed for genetic parallelism at the level of the SNP, gene, and paralog.

5.3 Methods

5.3.1 Sampling

Tissue samples (gill and fin) (N = 342, Table 5.1) were collected between 2010 and 2017 from landlocked and anadromous populations of Arctic Charr from five drainages in Labrador; these were, from north to south: Saglek Fjord, Hebron Fjord, Okak Region, Anaktalik River, and Voisey Bay (Fig.5.1). Landlocked populations (denoted as -L) were sampled using variable sized standardized nylon monofilament gillnets (1.27–8.89 cm diagonal) while anadromous populations (denoted as -A) were electrofished. Landlocked specimens were weighed (g), measured for fork length (mm) and assessed for sex and maturity. All samples were immediately stored in 95% ethanol or RNAlater.

5.3.2 Extraction, Sequencing, Genotyping and Quality Control

DNA was extracted using either a glassmilk protocol (modified from Elphinstone et al. 2003), a Phenol Chloroform protocol (modified from Sambrook and Russell 2006), or a Qiagen DNeasy 96 Blood and Tissue extraction kit (Qiagen) and quantified using QuantIT PicoGreen (Life Technologies).

DNA samples were sent to the Clinical Genomic Centre of Mount Sinai Hospital (Toronto, Canada) for sequencing using an 87k Affymetrix Axiom Array (Nugent et al. 2019). We employed the “best practices workflow” for a diploid organism in Axiom Analysis Suite (Version 4.0.1.9) to analyze the resulting .CEL genomic data files. After applying Axiom Analysis Suite QC we retained a total of N = 307 individuals (Table 5.1) for further analyses. We removed 321 SNPs from the analysis due to inconsistent scoring among replicate samples. For comparative purposes we also included in a subset of our analyses N = 178 samples reported in Salisbury et al. (2020) from three sites (lakes Ramah, Brooklyn, and Esker North) which were extracted and genotyped identically to the anadromous and landlocked populations considered in this study. These collections are indicated with a star in Fig 1.

A minor allele frequency (MAF) filter of 0.01 was applied using PLINK (Version 1.9; Chang et al. 2015) when investigating the population structure within each landlocked population, within each landlocked/anadromous population combination, and

across all landlocked and anadromous populations. PGDSpider (Version 2.1.1.5)(Lischer and Excoffier 2012) was used to convert between PLINK and Genepop files and the R package (R Core Team 2013) *genepopedit* (Stanley et al. 2017) was used to order and arrange Genepop files for downstream analyses.

5.3.3 Population Structure Analyses

We investigated for evidence of genetic sub-structuring, suggestive of incipient speciation, within each landlocked population. Landlocked populations were assessed for K = 1-5 with ADMIXTURE (Version 1.3; Alexander et al. 2009)) using 10 cross-validations. Landlocked samples in the northernmost drainage, Saglek Fjord (WP132 and WP133) were grouped together for ADMIXTURE analysis due to their close proximity and their previous noted genetic similarity (Salisbury et al. 2018). Landlocked samples in the southernmost drainage, Voisey Bay (SLU-L and GB-L) were grouped together for ADMIXTURE analysis due to their low sample sizes. For landlocked populations where the best K-value (that with the lowest average cross-validation error) was greater than 1, individuals were assigned to genetic groups based on ADMIXTURE Q-values. ANOVAs and posthoc Tukey's tests (α=0.05) were conducted to assess the effects of genetic group assignment and maturity on fork length (mm). Each genetic group detected within a single landlocked population was subsequently separately compared with the anadromous population within the same drainage. The genetic structure within landlocked lakes and between paired landlocked and anadromous populations within each drainage was assessed using 1) the R package *PCAdapt* (Version 4.1.0; Luu et al. 2017) testing K = 1-20 (K = 1-10 where the number of samples < 20) with the default Mahalanobis distance, and 2) the *snmf* function in the R package *LEA* (Frichot and François 2015) testing K = 1-5 using 10 repetitions. The population structure of all landlocked and anadromous populations was also assessed using *PCAdapt* testing K = 1-20, and weighted pairwise F_{ST}s were estimated between all populations using package *hierfstat* (Goudet 2005) (separating those sympatric, genetically differentiated morphs identified in landlocked populations). *PCAdapt* analyses (testing K=1-30) and weighted pairwise F_{ST} estimations were repeated to include all populations as well as the sympatric small (s) and big (b)

morphs identified in three lakes (Ramah, Brooklyn, Esker North) in Labrador by Salisbury et al. (2020) for a total of N = 485 samples.

5.3.4 Outlier Detection

Outlier SNPs were first detected using two methods. First, PCAdapt was used to detect outlier SNPs based on their correlation with the first PC axis after p-values were corrected using the False Discovery Rate (FDR; Storey and Tibshirani 2003) with the R package *qvalue* (Version 2.14.1; Storey 2015). Second, using Weir and Cockerham (1984) F_{ST}s estimated from PLINK, SNPs with an F_{ST} > 3 SD above the mean F_{ST} were considered outliers. Genes within 5000 bp of an outlier SNP were considered putative outliers subject to divergent selection.

The allelic frequencies of outlier SNPs detected within multiple landlocked populations and/or between multiple landlocked/anadromous population comparisons were visualized using the R package *ComplexHeatMap* (Gu et al. 2016). We assessed each outlier SNP for parallel allelic trends by determining the direction of the difference in major allele frequency (positive or negative) for outlier SNPs. An outlier SNP was considered to demonstrate parallel allelic trends if the directionality of this difference was the same in all such pairs for which the SNP was detected as an outlier.

We investigated whether there was evidence for divergent selection of different paralogous copies of genes both within and across locations. Specifically, we identified instances where multiple paralogs were associated with outlier SNPs 1) differentiating morphs within individual landlocked lakes, and 2) differentiating landlocked and anadromous populations within a single pair. We also examined whether different paralogs demonstrated signatures of selection in different landlocked populations or in different paired landlocked and anadromous populations. Such evidence would suggest the employment of different copies of the same gene to drive differentiation among replicate landlocked and replicate landlocked/anadromous pairs.

5.3.5 Gene Ontology Enrichment

Gene Ontology (GO) enrichment analyses for Biological Processes were conducted using the R package *TopGO* employing the protein GO annotation file

generated for an uncharacterized *Salvelinus sp.* (Christensen et al. 2018; NCBI assembly ASM291031v2) and formatted using BEDOPS (Neph et al. 2012). GO term significance was assessed with a Fisher's exact test using the "weight01" algorithm, p-values were corrected using FDR ($\alpha = 0.05$). The GO term universe for each analysis was limited to those SNPs located < 5000 bp from a gene within the genome for an uncharacterized *Salvelinus sp.* (Christensen et al. 2018; NCBI assembly ASM291031v2).

5.4 Results

5.4.1 Genetic differentiation within landlocked populations

The number of SNPs that passed filtering when considering single landlocked populations varied between N = 6404 in WP-L to N = 16702 in LO-L (Table S5.1). ADMIXTURE analyses supported within-lake genetic sub-structuring (where the best K > 1) in only WP-L and LO-L (Fig.5.2a,d, Table S5.2). Within WP-L, samples assigned to both genetic groups were found within each of the two neighbouring lakes (WP132-L and WP133-L), suggesting recent gene flow between these lakes despite the presence of intervening falls (Anderson 1985). While most individuals demonstrated high Q-values indicating strong support for their genetic assignment, six individuals in the WP-L lakes had intermediate Q-values (0.4 < Q-value < 0.6) suggesting they were hybrids. These putative hybrids were removed before conducting all outlier detection analyses to potentially more easily detect outlier loci and signatures of divergent selection between sympatric morphs. Pairwise mean (weighted) F_{ST} values between these ADMIXTURE-defined groups was 0.12 (0.16) within WP-L (calculated excluding putative hybrids) and 0.12 (0.18) within LO-L. ADMIXTURE-defined groups for each of WP-L and LO-L were identical to those detected from PCAdapt and *snmf* population structure analyses (Fig.S5.1 – S5.4). We found no evidence of sympatric differentiation within any of the other landlocked lakes in the three remaining drainages examined. Although for KNU-L the CV was marginally lower for K = 2 than K=1 ($\Delta = 0.00236$, Table S5.2) the result was driven by only two individuals (Fig.S5.5). We therefore consider KNU as K = 1. Within the Voisey Bay drainage, the most well-supported K-value for the landlocked locations (GB-L and SLU-L) was K = 2 (Table S5.2), but this structure corresponded to lake location (Fig.S5.6) and was thus not driven by sympatric differentiation within lakes.

5.4.2 Size differences between sympatric genetic groups

The genetic groups detected within each of WP-L and LO-L differed by fork length. In WP-L, significant differences in length were detected among the six combinations of maturity (mature or immature), assigned genetic group, and hybrid status (One-way ANOVA; $F_{(5,49)} = 71.50$, p-value < 0.001, based on N = 55 individuals after removing three individuals with unknown maturity status). Tukey's post-hoc tests revealed purebred individuals from one genetic group (mature and immature) were significantly (p-value < 0.001) longer than those in the other purebred genetic group (Fig.5.2e, Table 5.2). Putative hybrids detected in WP-L were larger than either of the "purebred" morphs (mean length (mm) = 385, 329, 145 for ADMIXTURE-assigned hybrid (N = 6), big (N = 24), and small (N = 28) morphs, respectively; Fig.5.2e, Table 5.2). In LO-L (N = 29) one genetic group was significantly shorter than the other [two-way ANOVA of the interaction between maturity (2 levels: mature or immature) and assigned genetic group on fork length $F_{(1,25)} = 71.50$, p-value < 0.001] (Fig.5.2b, Table 5.2). Within both WP-L and LO-L, each genetic group comprised mature and immature individuals of both sexes (Table 5.2). (See Table S5.3 for sex, maturity, glacial lineage for samples from other landlocked locations.) We refer to each genetic group within each of WP-L and LO-L as "small" (s) and "big" (b) morphs hereafter.

5.4.3 Outlier SNPs detected between sympatric genetic groups

The number of outlier SNPs between these sympatric genetic groups in WP-L (sWP-L vs. bWP-L) and LO-L (sLO-L vs. bLO-L) was N = 108 and N = 400, respectively (by one or both outlier detection methods) (Fig.5.2c, f). Outlier SNPs were detected in 22 linkage groups in WP-L and 37 linkage groups in LO-L. The number of SNPs detected by each method is reported by lake (Table S5.4). Only a single outlier SNP (AX-181980220) was detected between morphs in both WP-L and LO-L (Table S5.5). It was located within the VPS10 domain-containing receptor SorCS2 gene and demonstrated parallel allelic trends (i.e., the direction of the change in major allele frequency between sympatric big and small morphs was the same across lakes) (Fig.S5.7, Table S5.6).

There was no evidence of multiple paralogous copies containing outlier SNPs within WP-L, but there was such evidence for two genes in LO-L (Table S5.7). Across WP-L and LO-L, there were no instances where different paralogous copies of the same gene were found to differentiate sympatric morphs. We next compare the landlocked vs. allopatric anadromous populations within drainages.

5.4.4 Population structure of all landlocked and anadromous populations

After applying a MAF of 0.01 across samples from all landlocked and anadromous populations (N = 307), we retained N = 20874 SNPs. The first two PCs from our PCAdapt analysis explained a combined 23.52% of the data and separated all anadromous populations from all landlocked populations (Fig.5.3a). Landlocked populations demonstrated strong genetic distinctiveness, in contrast to the anadromous populations, which were generally genetically similar to each other. When including small and big morphs from Ramah, Brooklyn, and Esker North (N = 485 samples, N = 21201 SNPs after MAF of 0.01) *PCAdapt* results indicate big morphs from Ramah grouped with anadromous populations (Fig.5.3b). Small morphs from Ramah and big and small morphs from Brooklyn and Esker North, instead, demonstrated high genetic differentiation from anadromous populations.

Weighted pairwise F_{ST} estimates for the N = 307 dataset (Fig.S5.8) were nearly identical to those of the N = 485 dataset (Fig.5.3c) and supported the PCA results. These weighted pairwise F_{ST} estimates showed landlocked populations in Saglek and Hebron were generally most similar to the anadromous population within their drainage (SWA-A, IKA-A, respectively) (Fig.5.3c, Fig.S5.8). Landlocked populations in Okak, Anaktalik, and Voisey were more genetically similar to anadromous populations from other drainages than to the anadromous population within their drainage (K05-A, ANA-A, REI-A, respectively). However, this difference was very slight (<0.01 in Okak and Anaktalik, <0.05 in Voisey) and likely reflects the high degree of drift experienced by landlocked populations as well as the reduced sample sizes particularly for landlocked and anadromous populations within Voisey. We therefore compared landlocked and anadromous populations within drainages to attempt to minimize detection of genetic

differences potentially due to population structure and local adaptive differences across drainages.

5.4.5 Outlier SNPs detected between paired landlocked and anadromous populations

The number of SNPs that passed filtering for each landlocked versus anadromous population comparison varied between N = 17321 for GB-L vs. REI-A in Voisey Bay to N = 22540 in sLO-L vs. K05-A in the Okak region (Table S5.8). Mean (weighted) F_{ST} values between paired landlocked and anadromous populations from the same drainage ranged from 0.10 (0.15) between sLO-L vs. K05-A (Okak region) and 0.26 (0.39) between bWP-L vs. SWA-A (Saglek Fjord; Table S5.8). Significant genetic distances between paired landlocked and anadromous populations were confirmed by PCAdapt and *snmf* population structure analyses (Fig.S5.8-S5.11).

The number of SNPs detected as outliers between paired landlocked and anadromous populations ranged from N = 370 in BS-L vs. K05-A (Okak region) to N = 2296 in KNU-L vs. ANA-A (Anaktalik River; Fig.5.4, Table S5.8). Outlier SNPs were detected in 35 or more linkage groups in all comparisons (Table S5.8). The number of SNPs detected by each method and for a given number of methods is reported by lake in the Supporting Material (Table S5.9). Some outlier SNPs detected for a given lake were non-polymorphic in other lakes (Table S5.10).

A total of 6357 SNPs were detected as outliers in at least one of the seven landlocked vs. anadromous population comparisons (for WP-L and LO-L, a SNP was considered an outlier if it was detected as such in at least one comparison between the anadromous population and one of the two morphs (big or small)). Of these, none were detected in all seven comparisons, one SNP was detected as an outlier in six comparisons, 29 outlier SNPs were detected in five comparisons, 76 outlier SNPs in four comparisons, 356 outlier SNPs in three comparisons, 1269 outlier SNPs in two comparisons, and 4626 outlier SNPs in only one comparison. We limit our discussion to only those 30 outlier SNPs demonstrating the strongest evidence of parallelism that were detected in five or more of the seven landlocked vs. anadromous population comparisons. Of these 30 SNPs, 28 showed evidence of parallel allelic trends (i.e., the difference in major allele frequency

between landlocked and anadromous populations was in the same direction (positive or negative) for all landlocked vs. anadromous pairs for which the SNP was detected as an outlier) (Fig.5.5).

The 30 outlier SNPs detected in five or more of seven landlocked vs. anadromous population comparisons corresponded to 20 genes (Table 5.2). Two additional genes contained outlier SNPs detected in five or more landlocked vs. anadromous populations but the same SNP was not detected as an outlier in each comparison, for a total of 23 outlier genes detected in five or more landlocked vs. anadromous populations. No significant Biological Processes GO terms were enriched for these 23 genes (using a gene universe based on only those SNPs detected as polymorphic in five or more of the seven landlocked vs. anadromous comparisons) after adjusting p-values using FDR (Table S5.11).

Evidence of paralogous copies of the same gene containing outlier SNPs was found both within and across landlocked vs. anadromous comparisons. Within each landlocked vs. anadromous comparison the number of genes containing outlier SNPs in two or more paralogous copies ranged from N = 1 in the BS-L vs. K05-A comparison to N = 71 in bLO-L vs. K05-A comparison. For N = 317 genes, at least two of the seven landlocked vs. anadromous population comparisons demonstrated outlier SNPs in different paralogous copies of the same gene. Only 16 of these genes with different paralogous copies found to be outliers across landlocked vs. anadromous comparisons were detected as outliers in five or more landlocked vs. anadromous comparisons and none were detected in all seven landlocked vs. anadromous comparisons (Table S5.12).

5.5 Discussion

Our results support the genetic isolation of landlocked Arctic Charr populations in comparison with their anadromous counterparts as well as the presence of sympatric, genetically distinguishable morphs in two landlocked lakes. There was evidence for limited genetic parallelism between geographically paired landlocked and anadromous populations suggesting the potential for consistent divergent selection between such populations. However, drift may have contributed to the lack of evidence for parallel

genetic differences between genetically distinguishable, size-differentiated, sympatric morphs observed in each of two landlocked locations.

5.5.1 Charr Population Structure

Size-differentiated genetically distinguishable sympatric morphs were detected within two landlocked locations (WP-L and LO-L). Two genetically distinguishable morphs had previously been identified in each of the lakes comprising WP-L using 11 microsatellite markers (Salisbury et al. 2018). However, unlike the current study, no significant size difference was observed by Salisbury et al. (2018) between these genetically distinguishable morphs. This was a surprising result given that a subset of those samples analyzed using microsatellites in Salisbury et al. (2018) were analysed using SNPs in this study (N = 58). However, this discrepancy may have been due to the failure to remove putative hybrid individuals in Salisbury et al. (2018) and the anticipated greater assignment accuracy associated with 6404 SNPs in comparison to 11 microsatellites (see Fig.S5.12 for further details).

The ecological contexts of the genetically distinguishable size-differentiated sympatric morphs in WP-L and LO-L remain ambiguous. Genetically distinguishable size-differentiated non-migratory morphs of Arctic Charr have been observed within lakes in Alaska (May-Mcnally et al. 2015b) and Europe (Westgaard et al. 2004) as well as more geographically proximate locations in Newfoundland (Gomez-Uchida et al. 2008) and northern Quebec (Power et al. 2009). While the ecological relationships among sympatric morphs is unknown in WP-L and LO-L, their size difference is very similar to that observed between a genetically distinguishable small, littoral morph and a large benthic morph within Lake Aigneau in northern Quebec (Power et al. 2009). Additionally, previous observations have been made of sympatric small morphs and large, cannibalistic morphs in Charr Lake within Hebron Fjord, Labrador (Bouillon and Dempson 1989). Further investigation is required to uncover the ecology of these genetically distinguishable morphs as well as the environmental factors driving/maintaining this genetic differentiation. Such insights will be critical for a better understanding of whether it is the absence of divergent selective pressure or the absence

of genetic diversity that prevents such incipient speciation in other landlocked charr populations.

Though we think morphs likely arose in sympatry within these lakes, we cannot entirely rule out the possibility of recent allopatry with subsequent secondary contact. However, there was no evidence that glacial lineage played a role in the propensity for incipient speciation within landlocked lakes. We previously genotyped samples from WP-L and LO-L (some of which were also used in this study) for the D-loop mtDNA region to infer glacial lineage (Salisbury et al. 2019). We found all samples from WP-L were of the Atlantic lineage, whereas all samples from LO-L were of the Arctic lineage (Table S5.3). Therefore, sympatric morphs were not founded by different glacial lineages and populations colonized by either lineage could have sympatric morphs. However, the genetic isolation of these landlocked lakes could have resulted in the fixation of haplotypes of a single lineage even if both lakes were initially colonized by an ancestrally admixed population (of both Atlantic and Arctic lineages). Therefore, the genetic contribution of these lineages to incipient speciation remains unknown and requires further investigation.

The relative genetic distinctiveness of landlocked populations of Arctic Charr compared to anadromous populations observed here was consistent with our expectations of their isolation caused by a lack of gene flow. Similar observations have been made in allopatric landlocked (or freshwater resident) populations of many other diadromous species (e.g., Hindar et al. 1991; Palkovacs et al. 2008; Sandlund et al. 2014; Delgado et al. 2019). Interestingly, of those sea-accessible populations with sympatric big (putative anadromous) and small (putative resident) charr investigated in Salisbury et al. (2020) only the big morphs from Ramah but not those of Brooklyn or Esker North were genetically similar to the anadromous populations studied here. Though Anderson (1975) suggests both Esker North and Brooklyn are sea-accessible, given the remoteness of these lakes there is some uncertainty about this status particularly for Esker North which was considered landlocked by Van der Velden et al. (2012). It is possible then that big morphs from Esker North and perhaps even from Brooklyn could be non-anadromous, but as stated in Salisbury et al. (2020) it would be useful to verify the migratory phenotype of these morphs using telemetry, stable isotopes, etc. Regardless, the genetic distinctiveness

of Brooklyn and Esker North charr likely contributed to the limited genetic parallelism observed between sympatric small and big morphs across Ramah, Brooklyn, and Esker North (Salisbury et al. 2020).

5.5.2 Parallelism of Allopatric Genetic Differentiation Between Paired Landlocked and Anadromous Populations

Given the isolation of landlocked populations, genetic drift undoubtedly contributes to the high genetic differentiation between paired landlocked and anadromous populations and may have allowed for false positive detection of outlier loci in this study. We therefore limit our discussion of parallel genetic differentiation between landlocked and anadromous locations to those SNPs, genes, and paralogs demonstrating the strongest evidence of parallelism (detected in at least five of the seven paired comparisons).

Despite the isolated nature of landlocked populations and their likely experience of drift we find evidence for some parallel adaptive genetic differentiation between landlocked and anadromous populations. The majority of the outliers observed between at least five of the seven pairs of landlocked lakes and anadromous populations (28 of 30 SNPs) demonstrate parallel allelic trends. This supports the suggestion that these outlier loci (or those nearby which are physically linked) are responding to consistent directional selection experienced between landlocked and anadromous life-histories.

Of the genes containing one or more outlier loci in at least five of the seven comparisons, several have been previously associated with phenotypes consistent with the anticipated adaptive differences between landlocked and anadromous life-histories. The gene 1-acyl-sn-glycerol-3-phosphate acyltransferase gamma is associated with lipid biosynthesis in Atlantic Salmon (*Salmo salar*) (Morais et al. 2011). Several genes are associated with synapse development (neurexin-3a-like, extended synaptotagmin-1) (Rissone et al. 2007; Kikuma et al. 2017). The gene inactive dipeptidyl peptidase 10 is also associated with regulation of potassium in neurons (Jerng et al. 2004) and has intriguingly been found to genetically differentiate resident and diadromous populations of *Galaxias maculatus* in Chile (Delgado et al. 2019). Myomesin-2 is associated with cardiac and fast-twitch muscle function (Schoenauer et al. 2008) while lengsin is associated with vertebrate eye lens development (Wyatt et al. 2006). Six of the 23 genes

demonstrating parallelism also had paralogous copies which contained outlier SNPs (E3 ubiquitin-protein ligase BRE1B, extended synaptotagmin-1, neurexin-3a, parafibromin, PAN2-PAN3 deadenylation complex catalytic subunit PAN2, protocadherin-11 X-linked; Table 5.3, Table S5.12) further supporting the potential adaptive importance of these genes.

Interestingly, seven of the 30 outlier SNPs detected in at least five of the seven comparisons were also detected as an outlier between sympatric genetically distinguishable, small (putative resident) and large (putative anadromous) morphs in one of three Labrador lakes (Salisbury et al. 2020) (Fig.S5.13). These SNPs were associated with five outlier genes (Table S5.13). Five of these seven SNPs were in a ~240 kb region of AC17 and only detected as an outlier between sympatric morphs in the sea-accessible Ramah Lake (whose big, putative anadromous morphs were more genetically similar to the anadromous populations studied here than those big morphs from the other two lakes studied in Salisbury et al. (2020)). These SNPs were detected as outliers between landlocked and anadromous populations in the Okak, Anaktalik, and Voisey drainages, but not in the Saglek and Hebron drainages despite the geographical proximity of Ramah Lake to the latter two drainages. Despite this inconsistency, this region in AC17 might be important for differentiating anadromous and non-anadromous charr in both sympatry and allopatry.

Multiple genes demonstrated evidence for parallelism at the level of the paralog (for which different paralogous outlier loci were detected in different landlocked vs. anadromous population comparisons for five or more of seven comparisons). Most paralogs were located on distinct linkage groups although some paralogous copies were located on unmapped linkage groups and may not represent distinct paralogous copies. The presence of some paralogs on homeologous linkage groups suggests the potential importance of the recent whole genome duplication in salmonids (Macqueen and Johnston 2014) to contemporary adaptive differentiation. Several of these genes demonstrating parallelism at the level of the paralog were associated with ecologically relevant functions. One was chloride channel protein 2, which has been associated with osmoregulation and was differentially expressed in salinity-tolerant and salinity-sensitive populations of Sacramento Splittail (*Pogonichthys macrolepidotus*) (Jeffries et al. 2019;

Mundy et al. 2020). Another, pro-neuregulin-3, membrane-bound isoform is associated with neural development in mice (Anton et al. 2004; Zhang et al. 2014) and has been found to genetically differentiate migratory and non-migratory Brown Trout (*Salmo trutta*) (Lemopoulos et al. 2018). Paralogous copies of this gene were also found to genetically differentiate sympatric small and large morphs in each of three locations in Labrador (Salisbury et al. 2020) (Table S5.14). Four additional genes with evidence for parallelism at the level of the paralog were also found to differentiate sympatric small and big morphs of Arctic Charr in at least one of the three populations in Labrador studied by Salisbury et al. (2020) (Table S5.14). Paralogs of these genes may be employed to repeatably drive adaptive differentiation of migratory and non-migratory Arctic Charr in sympatry and allopatry.

It is noteworthy that no single gene or paralog was consistently differentiated between landlocked and anadromous populations across pairs and that the genes demonstrating parallelism were spread across the genome. These results thus differ from recent observations that a single locus of large effect dictates migration timing in Chinook Salmon (*Oncorhynchus nerka*) and Rainbow Trout (Prince et al. 2017) and that migratory life history in Rainbow Trout (*Oncorhynchus mykiss*) (Arostegui et al. 2019; Pearse et al. 2019) and in Japanese Grenadier Anchovy (*Coilia nasus*) (Zong et al. 2020) are associated with consistent genomic inversions. Similarly, consistent loci underly adaptive phenotypic traits (such as armoured plating and pelvic spines) in independent freshwater populations of Three-spined Stickleback (e.g., Nelson and Cresko 2018; Xie et al. 2019). Our observation of limited genetic parallelism could be due to local adaptation or the potential use of multiple genetic pathways to achieve a landlocked and an anadromous life history (Campbell and Bernatchez 2004). Because landlocked populations could have been established only within the last 9000 years BP (Bryson et al. 1969; Occhietti et al. 2011), some landlocked populations may not have had enough time to accumulate parallel genetic differences. Alternatively, any contemporary or historical connectivity with anadromous populations might have also impeded the adaptive differentiation of landlocked populations and prevented genetic parallelism. However, given the observed genetic distinctiveness and inferred isolation of landlocked

populations, we suggest that it is most likely that genetic drift has substantially limited genetic parallelism.

5.5.3 Parallelism of Sympatric Speciation Within Landlocked Lakes

The isolation of WP-L and LO-L is potentially responsible for the lack of repeated genetic differentiation at both the level of the paralog and the gene between big and small morphs across locations. However, a single outlier gene was detected in common in both WP-L and LO-L: VPS10 domain-containing receptor SorCS2. This gene is involved with neural development (Rezgaoui et al. 2001) and has been associated with protection of neurons from oxidative stress in mice (Malik et al. 2019) as well as aggression in chickens (Li et al. 2016). Interestingly, the same SNP (AX-181980220) within this gene identified as an outlier in both WP-L and LO-L was also identified as an outlier between sympatric big and small Arctic Charr morphs within a lake in Labrador (Esker North Lake; Salisbury et al. 2020). This SNP demonstrated parallel allelic trends between small and big morphs in WP-L, LO-L, and Esker North Lake (Fig.S5.14). This gene has also been found to genetically differentiate adfluvial "coaster" and fluvial, resident Brook Trout (*Salvelinus fontinalis*) (Elias et al. 2018) as well as between resident "black" Kokanee Salmon and river-spawning Sockeye Salmon (*Oncorhynchus nerka*) (Veale and Russello 2017b). We speculate that this gene may be important in contributing to incipient speciation in all three lakes and suggest that this gene warrants further study of its developmental context and consequences. Four genes were also identified as outliers between sympatric small and big morphs in at least three locations from either the landlocked locations from this study (WP-L, LO-L) or the locations from Salisbury et al. (2020) (Ramah, Brooklyn, Esker North) (Table S5.15). Interestingly, the gene pappalysin-2, which has been associated with growth in mice and humans (Conover et al. 2011; Dauber et al. 2016), and was detected as an outlier between small and big morphs in all locations studied by Salisbury et al. (2020), was not detected as an outlier in either of WP-L or LO-L (Fig.S5.14, Table S5.15). Paralogous copies from two genes were identified as outliers within either WP-L or LO-L and in at least two of the locations from Salisbury et al. (2020) (Table S5.16).

5.5.4 Conclusions

Despite the isolation of landlocked populations, our results demonstrate that their genetic diversity was sufficient to allow for both incipient speciation as well as their consistent, potentially adaptive genetic differentiation from anadromous populations. While the former result has previously been observed (e.g., Guðbrandsson et al. 2019; Jacobs et al. 2020; Østbye et al. 2020), the latter has rarely been assessed using a replicated pairwise design of natural populations as studied here. Our experimental design allowed us to uncover a number of candidate genes and paralogs demonstrating genetic parallelism across drainages, many of which were associated with ecologically relevant functions. Furthermore, some of the genes we observed to consistently genetically differentiate landlocked and anadromous populations had also previously been found to differentiate sympatric putative resident and putative anadromous Arctic Charr in other Labrador populations. Some of these genes had also been associated with migratory and non-migratory life histories in other fish species. Our results propose the intriguing possibility that migration in Arctic Charr and other fishes may share a common genetic underpinning.

5.6 Author Contributions

SJS and DER conceptualized the study. SJS, DER, RP, DK, IRB developed and conducted sampling design. SJS and GRM conducted lab work. JSL, CMN, BFK, and MMF contributed to the data collection (sequencing and genotyping). DER, GRM, IRB, KKSL, TK contributed to data analysis, visualization, and interpretation. SJS analyzed data and led the writing under the supervision of DER. All authors contributed to editing the paper.

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5.8 Tables

Table 5.1 Details of sampling locations for landlocked (L) and anadromous (A) populations.

Code	Location	Drainage	Population Type	Latitude	Longitude	Sampling Year(s)	N	N Passing QC
SWA-A	Southwest Arm	Saglek	A	58.46825	-63.64623	2017	30	30
WP-L	WP133-L	Saglek	L	58.27167	-64.03136	2014	28	28
	WP132-L	Saglek	L	58.28016	-63.9693	2014	30	30
IKA-A	Ikarut River	Hebron	A	58.16057	-63.16141	2017	30	25
HEB-L	Hebron Lake	Hebron	L	58.14611	-63.59133	2015	30	30
K05-A	North River	Okak	A	57.50159	-62.74318	2015	30	29
BS-L	Beachy Strip Lake	Okak	L	57.66161	-62.95445	2015	30	29
LO-L	Lonely Lake	Okak	L	57.63915	-63.23292	2015	30	29
ANA-A	Anaktalik River	Anaktalik	A	56.49753	-62.93309	2017	30	30
KNU-L	Knumandi Lake	Anaktalik	L	56.58141	-63.32335	2011	20	16
REI-A	Reid Brook	Voisey	A	56.30319	-62.08522	2017	30	9
SLU-L	Slushy Lake	Voisey	L	56.41561	-64.10225	2010, 2011, 2012, 2013	11	10
GB-L	Genetics B Lake	Voisey	L	56.11067	-63.38858	2010, 2011	13	12
						Totals	**342**	**307**

Table 5.2 Number of small and big morph Arctic Charr samples detected within landlocked locations WP-L and LO-L. Arctic and Atlantic lineage haplotypes from Salisbury et al. (2019). Note that the sum of all immature/mature males/females may not equal N, as some samples had unknown maturity status.

Location	Morph	Code	N	Mean (Median) Length (mm)	Immature Males	Immature Females	Mature Males	Mature Females	Atlantic Lineage	Arctic Lineage
WP-L	small	sWP-L	28	145 (136)	6	4	7	9	15	0
	big	bWP-L	24	329 (352)	8	8	3	4	14	0
	hybrid	hWP-L	6	385 (372)	1	1	3	1	4	0
LO-L	small	sLO-L	21	145 (125)	2	4	8	7	0	16
	big	bLO-L	8	328 (303)	3	3	1	1	0	7

Table 5.3 Genes detected as outliers in five or more of seven landlocked vs. anadromous population comparisons (1) WP-L vs. SWA-A (either sWP-L vs. SWA-A or bWP-L vs. SWA-A), 2) HEB-L vs. IKA-A, 3) BS-L vs. K05-A, 4) LO-L vs. K05-A (either sLO-L vs. K05-A or bLO-L vs. K05-A), 5) KNU-L vs. ANA-A, 6) SLU-L vs. REI-A, 7) GB-L vs. REI-A). The method by which each SNP was identified as an outlier is denoted for each landlocked vs. anadromous population comparison (P – PCAdapt, F- F_{ST}).

						Method by which outlier was detected								
Gene Name	Linkage Group	Protein Code	SNP Code	Position (bp)	Position Relative to CDS (bp)	sWP -L vs. SWA-A	bWP-L vs. SWA-A	HEB-L vs. IKA-A	BS-L vs. K05-A	sLO-L vs. K05-A	bLO-L vs. K05-A	KNU-L vs. ANA-A	SLU-L vs. REI-A	GB-L vs. REI-A
1-acyl-sn-glycerol-3-phosphate acyltransferase gamma	AC02	XP_023860472.1	AX-181934436	17123421	0		P	P			P,F	P	P,F	P,F
neurexin-3a-like	AC04q.2	XP_023842075.1	AX-181947935	28835631	0								P,F	
			AX-181915470	28938899	0	P		P		F	P	P		
			AX-181937420	29244795	0	P	P							

Table 5.3 Continued.

Gene Name	Linkage Group	Protein Code	SNP Code	Position (bp)	Position Relative to CDS (bp)	Method by which outlier was detected								
						sWP -L vs. SWA-A	bWP-L vs. SWA-A	HEB-L vs. IKA-A	BS-L vs. K05-A	sLO-L vs. K05-A	bLO-L vs. K05-A	KNU-L vs. ANA-A	SLU-L vs. REI-A	GB-L vs. REI-A
LOW QUALITY PROTEIN: protocadherin-11 X-linked-like	AC08	XP_023847824.1	AX-181937960	798438	0	P	P				P	P	P	P,F
extended synaptotagmin-1	AC11	XP_023852472.2	AX-181939957	30693817	0			P	P,F	P,F	P,F	P	P,F	
E3 ubiquitin-protein ligase DTX3L isoform X1	AC11	XP_023852474.1	AX-181933794	30720520	0			P	P,F	P,F	P,F	P	P,F	
			AX-181933793	30720968	0			P	P,F	P,F	P,F	P	P,F	
			AX-181941389	30724186	-946			P	P,F	P,F	P,F	P	P,F	
EEF1A lysine methyltransferase 3 isoform X2	AC11	XP_023852598.1	AX-181922045	32818906	584		P		F		P,F	P	P,F	
uncharacterized protein LOC111970338	AC11	XP_023852785.1	AX-181945827	38551900	-4540	P			F		P	P	P	
partner of Y14 and mago B	AC17	XP_023861958.1	AX-181916308	22616133	98				P,F	P,F	P,F	P	P,F	P,F
			AX-181916309	22616560	0				P,F	P,F	P,F	P	P,F	P,F
PAN2-PAN3 deadenylation complex catalytic subunit PAN2 isoform X1	AC17	XP_023861482.1	AX-181952107	22685483	-2559				P,F	P,F	P,F	P,F	P	P,F
nuclear envelope integral membrane protein 1-like isoform X1	AC17	XP_023862374.1	AX-181967022	22704350	0				P,F	P,F	P,F	P	P,F	P,F

Table 5.3 Continued.

Gene Name	Linkage Group	Protein Code	SNP Code	Position (bp)	Position Relative to CDS (bp)	Method by which outlier was detected								
						sWP -L vs. SWA-A	bWP-L vs. SWA-A	HEB-L vs. IKA-A	BS-L vs. K05-A	sLO-L vs. K05-A	bLO-L vs. K05-A	KNU-L vs. ANA-A	SLU-L vs. REI-A	GB-L vs. REI-A
LOW QUALITY PROTEIN: serine/threonine-protein phosphatase 6 regulatory ankyrin repeat subunit C-like	AC17	XP_023862177.1	AX-181980622	22869580	2738				P,F	F	P,F	P	P,F	P,F
			AX-181983398	22869600	2718				P,F	F	P,F	P	P,F	P,F
inactive dipeptidyl peptidase 10	AC17	XP_023860785.1	AX-182162437	22923504	0				P,F	P,F	P,F	P	P,F	P,F
			AX-181987181	22950203	0				P,F	P,F	P,F	P		P,F
E3 ubiquitin-protein ligase BRE1B isoform X2	AC18	XP_023862569.1	AX-181935230	13010818	0			P,F	P,F	P,F		P		P
			AX-181935231	13016862	0			P,F	P,F	P,F		P		
parafibromin	AC19	XP_023865178.1	AX-181969955	34116352	0	P	P	P,F	P	F		P		
calpain-9	AC21	XP_023869744.1	AX-181973095	1423711	0	P	P	P,F	P,F	P,F	P	P		
uncharacterized protein LOC111982472	AC21	XP_023869810.1	AX-181936535	2E+06	0	P	P	P,F	P,F	P,F	P	P		
myomesin-2	AC21	XP_024003594.1	AX-181973093	1549701	0	P	P	P		P,F	P,F	P		P
			AX-181936531	1560037	-1756	P	P	P		P,F	P,F	P		P
LOW QUALITY PROTEIN: lengsin	AC21	XP_023869550.1	AX-181936530	1565479	838	P	P	P		P,F	P,F	P		P
peroxisome assembly protein 12	AC23	XP_023824703.1	AX-181933438	19272943	0	P	P				P	P	P,F	P,F

Table 5.3 Continued.

Gene Name	Linkage Group	Protein Code	SNP Code	Position (bp)	Position Relative to CDS (bp)	Method by which outlier was detected								
						sWP -L vs. SWA-A	bWP-L vs. SWA-A	HEB-L vs. IKA-A	BS-L vs. K05-A	sLO-L vs. K05-A	bLO-L vs. K05-A	KNU-L vs. ANA-A	SLU-L vs. REI-A	GB-L vs. REI-A
exonuclease V-like isoform X2	AC23	XP_023823204.1	AX-181933434	19698413	0	P	P				P	P	P,F	P,F
collagen alpha-1(XXVI) chain-like	AC23	XP_023823891.1	AX-182165632	20027708	-3226	P	P				P	P	P,F	P,F
ubl carboxyl-terminal hydrolase 18-like	AC24	XP_023825191.1	AX-181937172	9642671	-253	P	P			P,F	P	P	P,F	P
			AX-181944480	9644323	-1905	P	P			P,F				
DET1- and DDB1-associated protein 1	AC32	XP_023833368.1	AX-181924007	10264014	-1187		P				P	P		
			AX-181924006	10264039	-1212			P						P

5.9 Figures

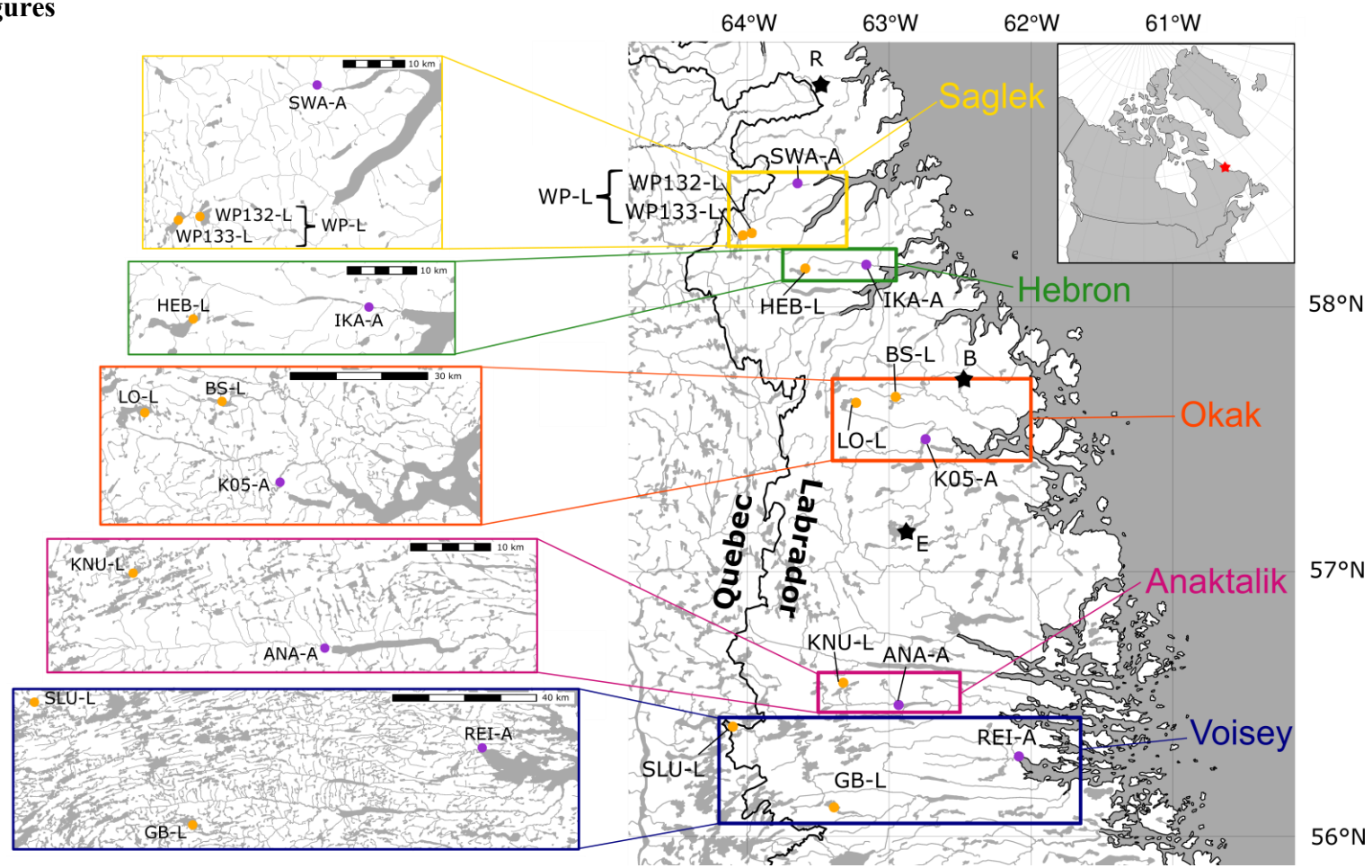


Fig.5.1 Sampling locations in Labrador, Canada in five localities: Saglek Fjord, Hebron Fjord, Okak Region, Anaktalik River, Voisey Bay. Within each drainage, orange circles indicate landlocked Arctic Charr (*Salvelinus alpinus*) populations, purple circles indicate anadromous Arctic Charr populations. Black stars indicate lakes from Salisbury et al. (2020) (R-Ramah, B-Brooklyn, E-Esker North). Map generated using data from CanVec (Government of Canada).

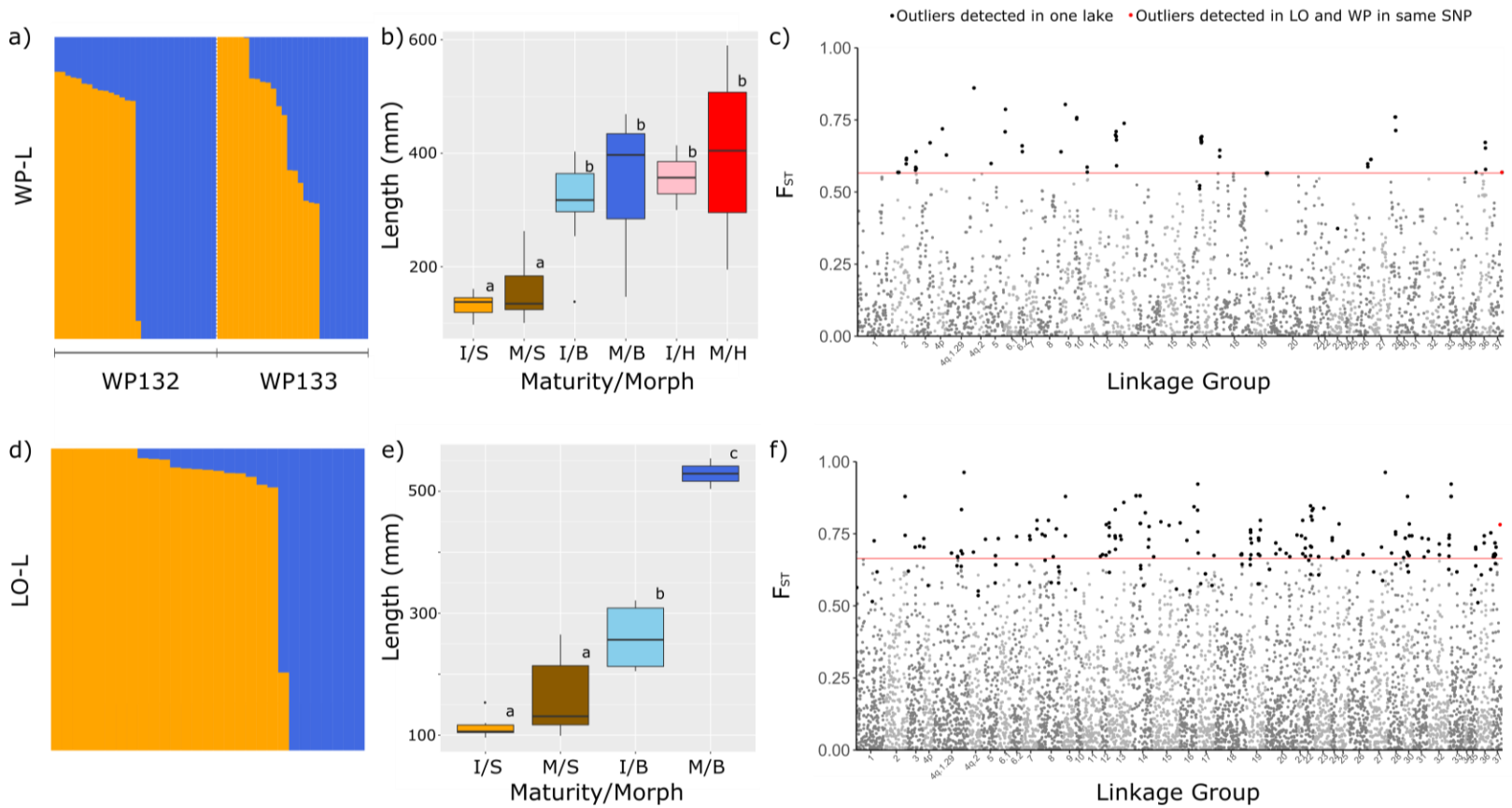
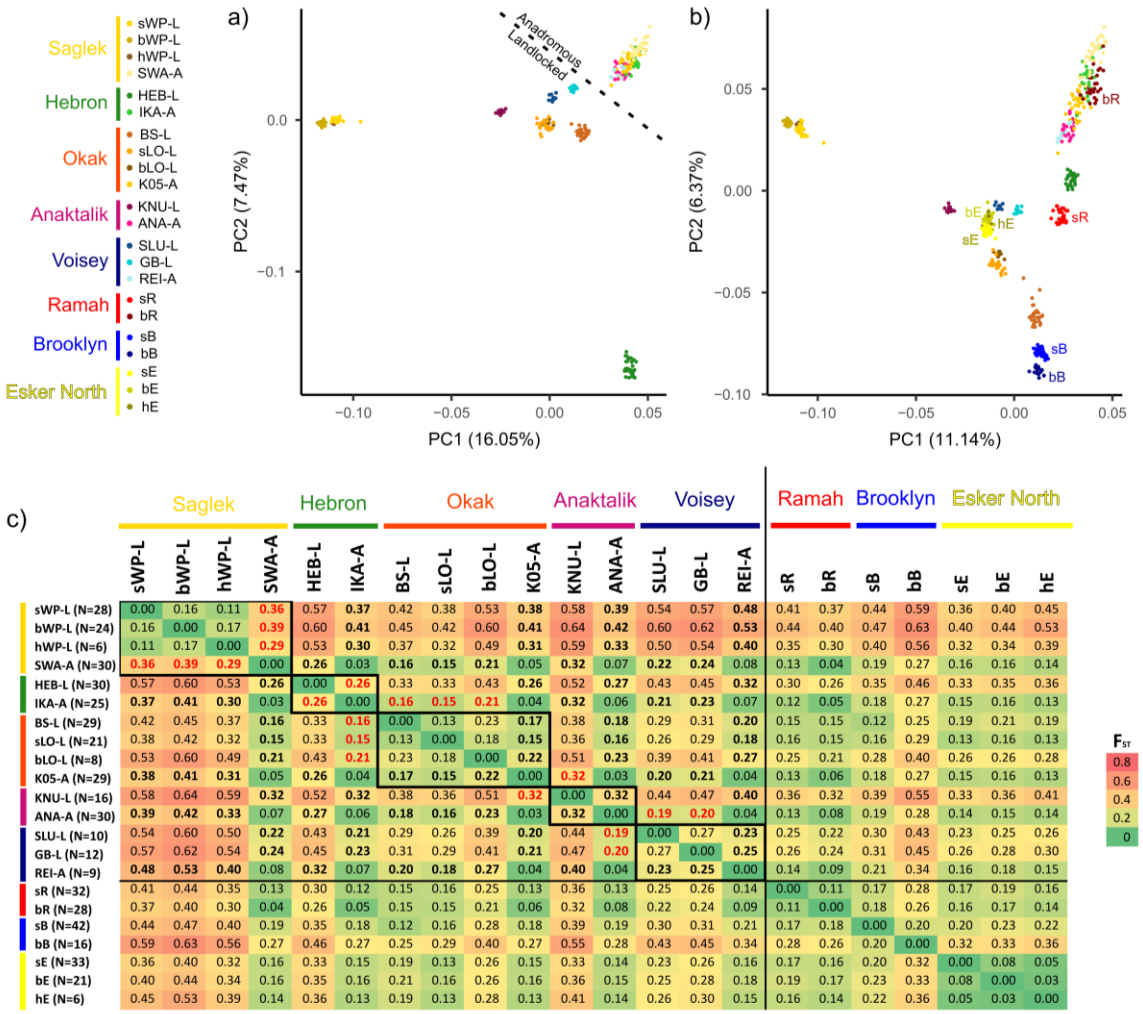


Fig.5.2 ADMIXTURE plots of K = 2 for a) WP-L and d) LO-L. Orange bars indicate small morph individuals, blue bars indicate big morph individuals. Boxplots demonstrating length of fish by maturity (immature (I), mature (M)) and morph type (small (S), big (B), hybrid (H)) in b) WP-L (N = 55) and e) LO-L (N = 29). Shared letters among boxplots indicate a lack of statistical difference (α = 0.05) after a Tukey HSD test. Manhattan plots demonstrating F_{ST} values of outlier loci detected in c) WP-L and f) LO-L. Red lines indicate 3 standard deviation above the mean F_{ST} and detected outliers are highlighted.



	sWP-L	bWP-L	hWP-L	SWA-A	HEB-L	IKA-A	BS-L	sLO-L	bLO-L	K05-A	KNU-L	ANA-A	SLU-L	GB-L	REI-A	sR	bR	sB	bB	sE	bE	hE
sWP-L (N=28)	0.00	0.16	0.11	0.36	0.57	0.37	0.42	0.38	0.53	0.38	0.58	0.39	0.54	0.57	0.48	0.41	0.37	0.44	0.59	0.36	0.40	0.45
bWP-L (N=24)	0.16	0.00	0.17	0.39	0.60	0.41	0.45	0.42	0.60	0.41	0.64	0.42	0.60	0.62	0.53	0.44	0.40	0.47	0.63	0.40	0.44	0.53
hWP-L (N=6)	0.11	0.17	0.00	0.29	0.53	0.30	0.37	0.32	0.49	0.31	0.59	0.33	0.50	0.54	0.40	0.35	0.30	0.40	0.56	0.32	0.34	0.39
SWA-A (N=30)	0.36	0.39	0.29	0.00	0.26	0.03	0.16	0.15	0.21	0.05	0.32	0.07	0.22	0.24	0.08	0.13	0.04	0.19	0.27	0.16	0.16	0.14
HEB-L (N=30)	0.57	0.60	0.53	0.26	0.00	0.26	0.33	0.33	0.43	0.26	0.52	0.27	0.43	0.45	0.32	0.30	0.26	0.35	0.46	0.33	0.35	0.36
IKA-A (N=25)	0.37	0.41	0.30	0.03	0.26	0.00	0.16	0.15	0.21	0.04	0.32	0.06	0.21	0.23	0.07	0.12	0.05	0.18	0.27	0.15	0.16	0.13
BS-L (N=29)	0.42	0.45	0.37	0.16	0.33	0.16	0.00	0.13	0.23	0.17	0.38	0.18	0.29	0.31	0.20	0.15	0.15	0.12	0.25	0.19	0.21	0.19
sLO-L (N=21)	0.38	0.42	0.32	0.15	0.33	0.15	0.13	0.00	0.18	0.15	0.36	0.16	0.26	0.29	0.18	0.16	0.15	0.16	0.29	0.13	0.16	0.13
bLO-L (N=8)	0.53	0.60	0.49	0.21	0.43	0.21	0.23	0.18	0.00	0.22	0.51	0.23	0.39	0.41	0.27	0.25	0.21	0.28	0.40	0.26	0.26	0.28
K05-A (N=29)	0.38	0.41	0.31	0.05	0.26	0.04	0.17	0.15	0.22	0.00	0.32	0.03	0.20	0.21	0.04	0.13	0.06	0.18	0.27	0.15	0.16	0.13
KNU-L (N=16)	0.58	0.64	0.59	0.32	0.52	0.32	0.38	0.36	0.51	0.32	0.00	0.32	0.44	0.47	0.40	0.36	0.32	0.39	0.55	0.33	0.36	0.41
ANA-A (N=30)	0.39	0.42	0.33	0.07	0.27	0.06	0.18	0.16	0.23	0.03	0.32	0.00	0.19	0.20	0.04	0.13	0.08	0.19	0.28	0.14	0.15	0.14
SLU-L (N=10)	0.54	0.60	0.50	0.22	0.43	0.21	0.29	0.26	0.39	0.20	0.44	0.19	0.00	0.27	0.23	0.25	0.22	0.30	0.43	0.23	0.25	0.26
GB-L (N=12)	0.57	0.62	0.54	0.24	0.45	0.23	0.31	0.29	0.41	0.21	0.47	0.20	0.27	0.00	0.25	0.26	0.24	0.31	0.45	0.26	0.28	0.30
REI-A (N=9)	0.48	0.53	0.40	0.08	0.32	0.07	0.20	0.18	0.27	0.04	0.40	0.04	0.23	0.25	0.00	0.14	0.09	0.21	0.34	0.16	0.18	0.15
sR (N=32)	0.41	0.44	0.35	0.13	0.30	0.12	0.15	0.16	0.25	0.13	0.36	0.13	0.25	0.26	0.14	0.00	0.11	0.17	0.28	0.17	0.19	0.16
bR (N=28)	0.37	0.40	0.30	0.04	0.26	0.05	0.15	0.15	0.21	0.06	0.32	0.08	0.22	0.24	0.09	0.11	0.00	0.18	0.26	0.16	0.17	0.14
sB (N=42)	0.44	0.47	0.40	0.19	0.35	0.18	0.12	0.16	0.28	0.18	0.39	0.19	0.30	0.31	0.21	0.17	0.18	0.00	0.20	0.20	0.23	0.22
bB (N=16)	0.59	0.63	0.56	0.27	0.46	0.27	0.25	0.29	0.40	0.27	0.55	0.28	0.43	0.45	0.34	0.28	0.26	0.20	0.00	0.32	0.33	0.36
sE (N=33)	0.36	0.40	0.32	0.16	0.33	0.15	0.19	0.13	0.26	0.15	0.33	0.14	0.23	0.26	0.16	0.17	0.16	0.20	0.32	0.00	0.08	0.05
bE (N=21)	0.40	0.44	0.34	0.16	0.35	0.16	0.21	0.16	0.26	0.16	0.36	0.15	0.25	0.28	0.18	0.19	0.17	0.23	0.33	0.08	0.00	0.03
hE (N=6)	0.45	0.53	0.39	0.14	0.36	0.13	0.19	0.13	0.28	0.13	0.41	0.14	0.26	0.30	0.15	0.16	0.14	0.22	0.36	0.05	0.03	0.00

Fig.5.3 Population structure of landlocked (L) (with sympatric morphs separated: small-s, big-b, hybrid-h), anadromous (A), and three sea-accessible lakes (Ramah-R, Brooklyn-B, Esker North-E) with sympatric morphs (small-s, big-b, hybrid-h) as detected by Salisbury et al. 2020: a) PCA of only L and A populations based on N = 20874 SNPs b) PCA of L and A population in addition to sea-accessible populations from Salisbury et al. 2020 (R, B, E; labeled by morph type for clarity) based on N = 21201 SNPs, c) weighted pairwise Weir and Cockerham (1984) F_{ST}s between all L, A, and sea-accessible populations (R, B, E) based on N=21201 SNPs. F_{ST}s estimated between landlocked and anadromous populations are bolded. Those F_{ST}s highlighted in red correspond to the lowest F_{ST} calculated between a given landlocked population and any of the anadromous populations. F_{ST} values estimated between populations within the same drainage are within bolded black boxes.

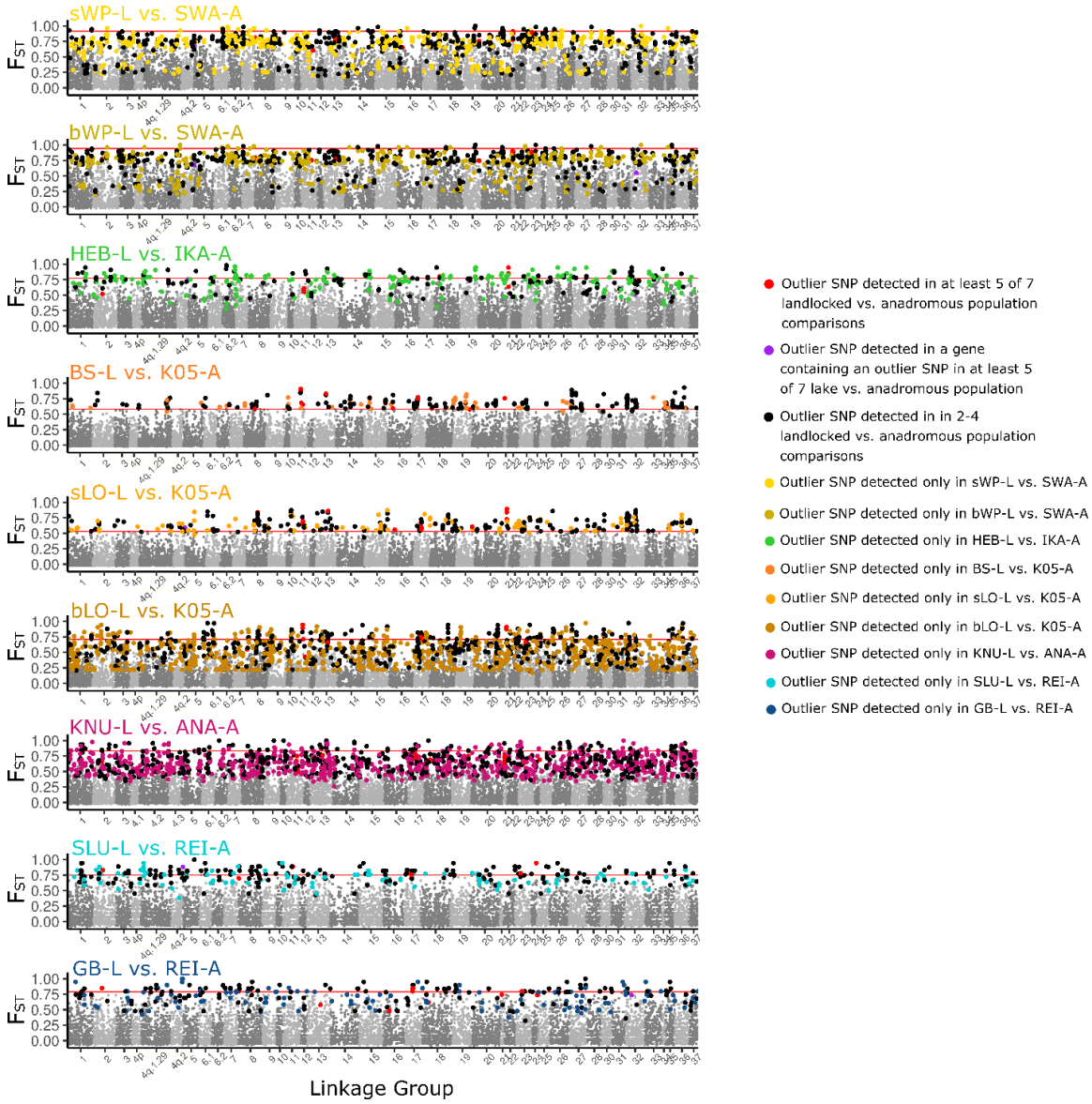


Fig.5.4 Manhattan plots demonstrating F_{ST} values of outlier loci detected between landlocked vs. anadromous populations. Red lines indicate 3 standard deviation above the mean F_{ST}. Note that mean pairwise F_{ST} was calculated separately for each of the two genetic subgroups (corresponding to small (s) and big (b) morphs) within each of LO and WP. However, outlier SNPs detected between either morph and the corresponding anadromous population were pooled when identifying SNPs detected in multiple landlocked vs. anadromous comparisons. Therefore, we identified outlier SNPs detected in 2-4 (black points) and in five or more (red points) of seven landlocked vs. anadromous populations: 1) WP-L vs. SWA-A (either sWP-L vs. SWA-A or bWP-L vs. SWA-A), 2) HEB-L vs. IKA-A, 3) BS-L vs. K05-A, 4) LO-L vs. K05-A (either sLO-L vs. K05-A or bLO-L vs. K05-A), 5) KNU-L vs. ANA-A, 6) SLU-L vs. REI-A, 7) GB-L vs. REI-A.

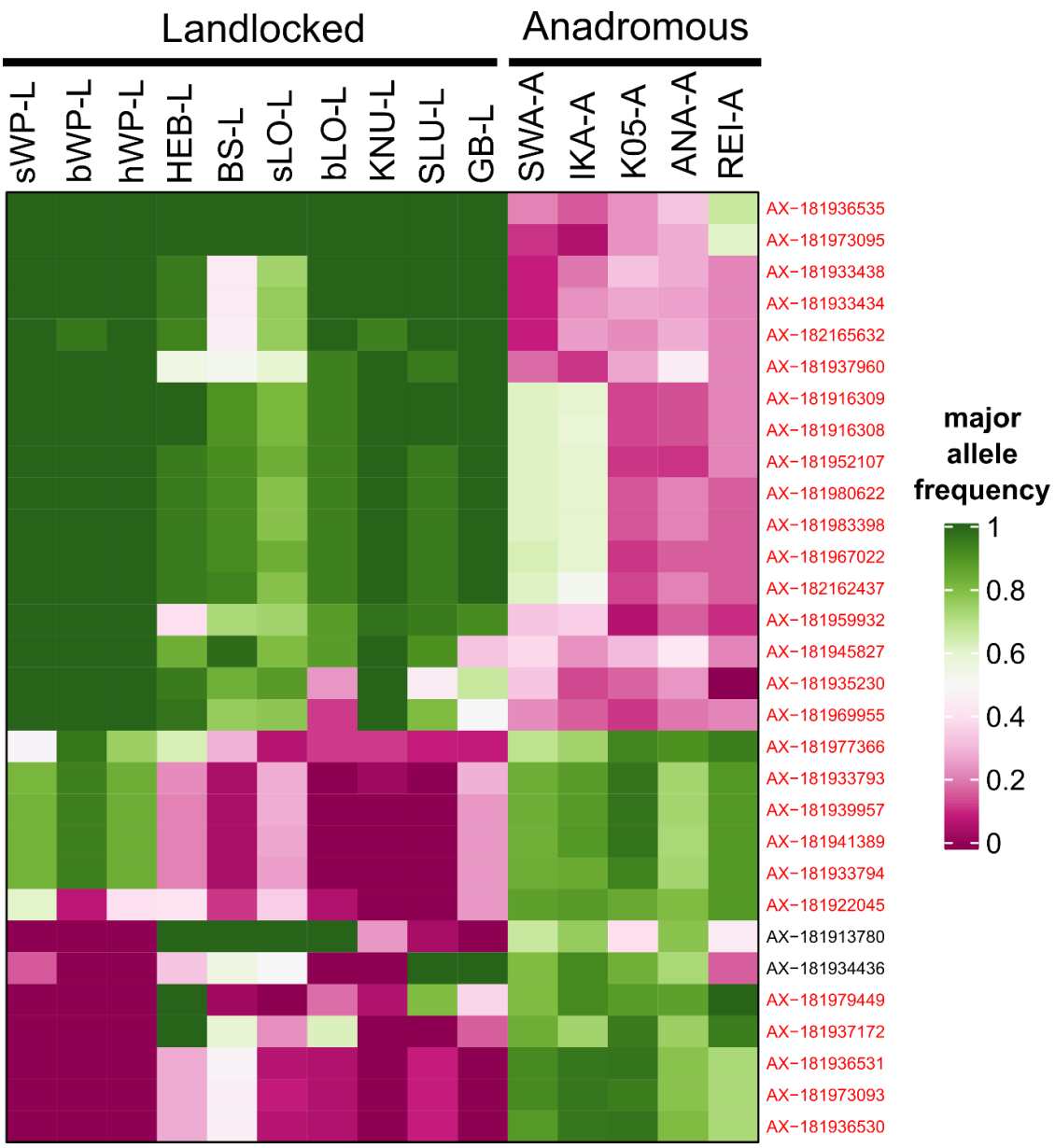


Fig.5.5 Heatmap of allele frequencies for those loci detected as outliers for five or more of seven paired landlocked and anadromous populations: 1) WP-L vs. SWA-A (either sWP-L vs. SWA-A or bWP-L vs. SWA-A), 2) HEB-L vs. IKA-A, 3) BS-L vs. K05-A, 4) LO-L vs. K05-A (either sLO-L vs. K05-A or bLO-L vs. K05-A), 5) KNU-L vs. ANA-A, 6) SLU-L vs. REI-A, 7) GB-L vs. REI-A. The names of SNPs which show parallel allelic trends across the locations in which a SNP was detected as an outlier are highlighted in red.

5.10 Supporting Information

5.10.1 Genotyping Details

When using Axiom Analysis Suite to genotype samples we used default sample quality control thresholds: dish quality control ≥ 0.82, quality control call rate ≥ 0.97, and average call rate of passing samples on a given plate ≥ 0.985. We regenerated SNP Metrics using the "Run PS Supplemental" option as recommended (Axiom Analysis Suite User manual version 3.1) for complex genomes to screen out putative paralogous sequence variants given the potential that some regions of the charr genome may remain un-diploidized after the salmonid whole genome duplication. Those SNPs categorized as "PolyHighResolution", "NoMinorHom" and "MonoHighResolution" were used in analyses. Samples from 2010-2015 were extracted in a different lab and sequenced at a separate time from the 2017 samples and were therefore analyzed as separate "batches" in accordance with Axiom Analysis Suite User manual (version 3.1). Four samples from the 2010-2015 batch were sequenced and genotyped two times in order to allow for the screening out of those SNPs which were not identically genotyped within individuals, however both replicates passed quality control measures in only three of these samples. Replicate genotypes of a single individual were combined for those SNPs where one of the two replicates was missing a genotype. Most landlocked populations were analysed in one batch, while the second batch was comprised of mostly anadromous populations. Therefore, when conducting pairwise comparisons between landlocked and anadromous populations SNPs with a frequency of one particular allele > 0.95 in one batch but < 0.05 in another were removed in order to exclude those SNPs that were genotyped inconsistently across the two batches used in this study.

Table S5.1 Number of SNPs which passed filtering within each landlocked location.

Location	N SNPs
WP-L	6404
HEB-L	10980
BS-L	16069
LO-L	16702
KNU-L	7378
Voisey Bay Landlocked (GB-L and SLU-L)	13886

Table S5.2 Average cross-validation error estimates for ADMIXTURE results for each lake and K-value. Lowest values for each lake are shaded.

K	WP-L (N = 6404 SNPs)	HEB-L (N = 10980 SNPs)	BS-L (N = 16069 SNPs)	LO-L (N = 16702 SNPs)	KNU-L (N = 7378 SNP)	Voisey Bay Landlocked (SLU-L and GB-L) (N = 13886 SNPs)
1	0.58803	0.59508	0.59270	0.63386	0.65604	0.67043
2	0.52533	0.62951	0.64830	0.61114	0.65368	0.61211
3	0.5439	0.71219	0.78784	0.66757	0.84033	0.81138
4	0.55642	0.80263	1.08615	0.80034	1.18553	0.88846
5	0.56519	0.97839	1.13428	0.95716	1.65730	1.15537

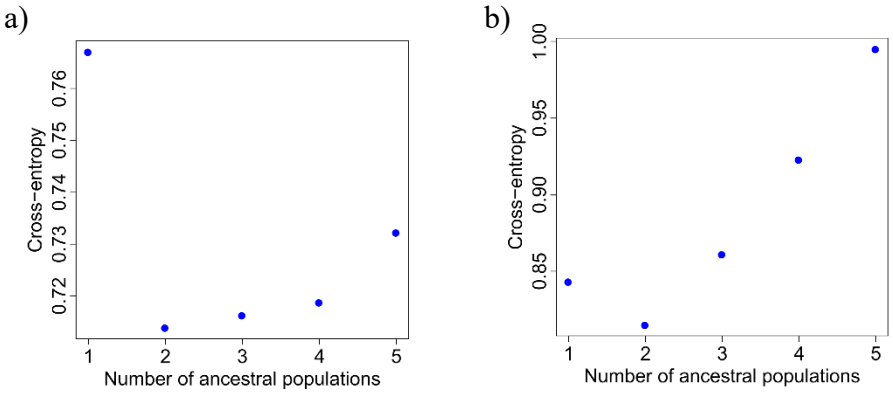


Fig.S5.1 SNMF cross-entropy values for K = 1-5 for a) WP-L, b) LO-L.

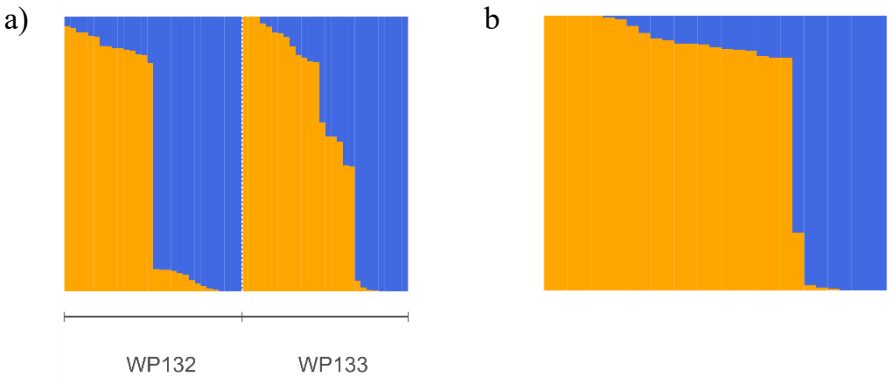


Fig.S5.2 SNMF plots of K = 2 for a) WP-L, b) LO-L. Orange bars indicate small morph samples, blue bars indicate big morph samples.

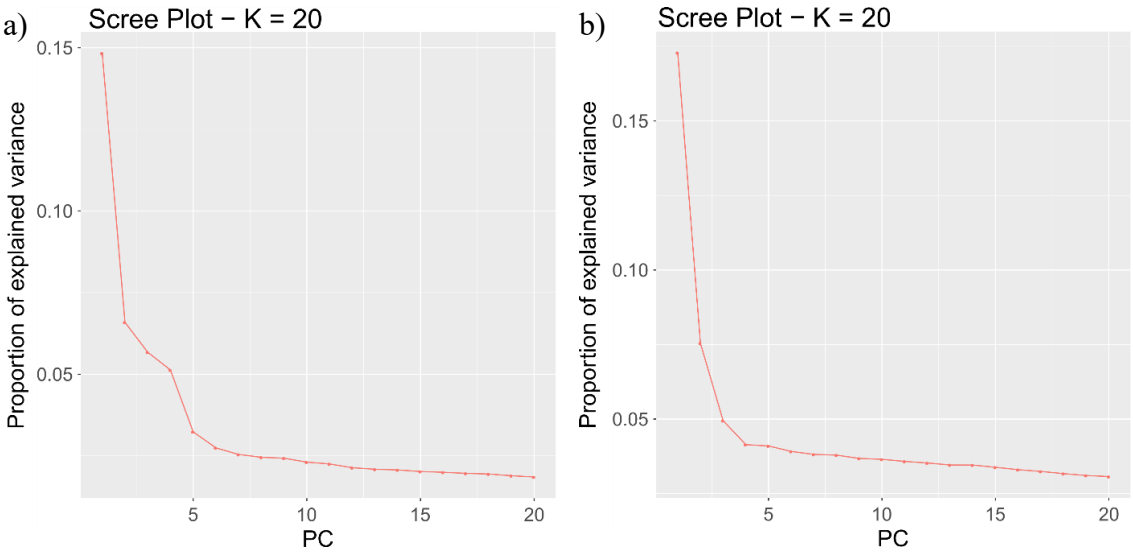


Fig.S5.3 Proportion of explained variance for each PC of PCAdapt population structure analysis for a) WP-L, b) LO-L.

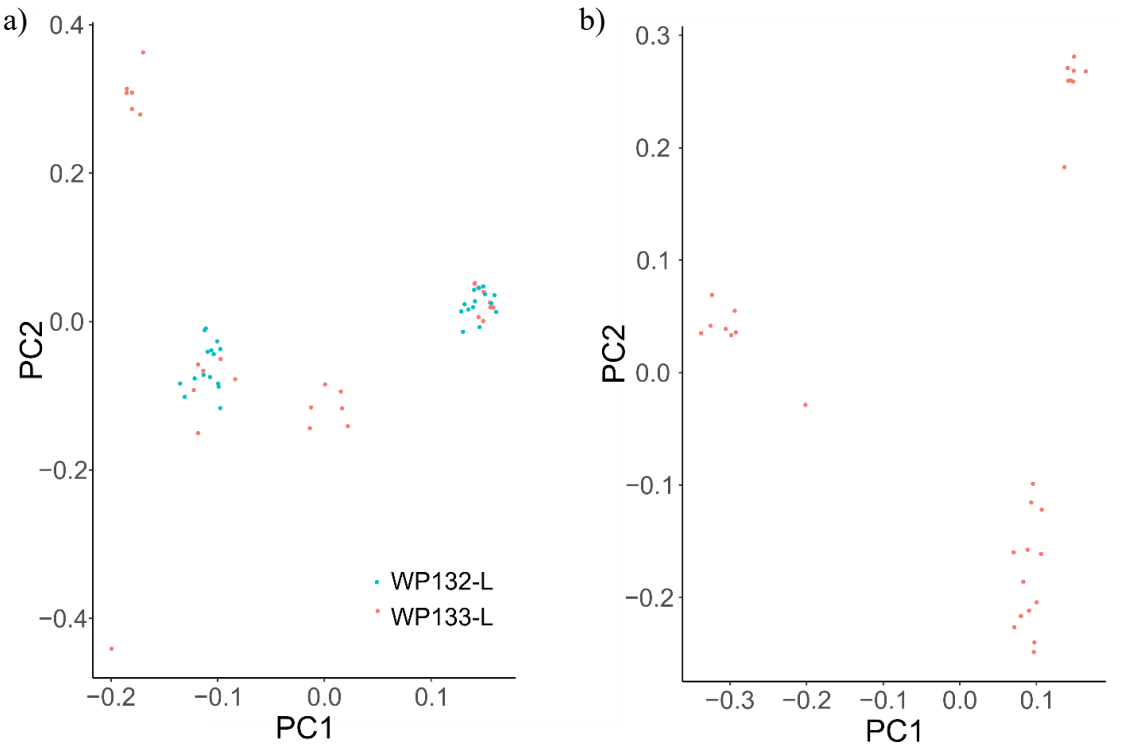


Fig.S5.4 Proportion of explained variance for each PC of PCAdapt population structure analysis for a) WP-L, b) LO-L.

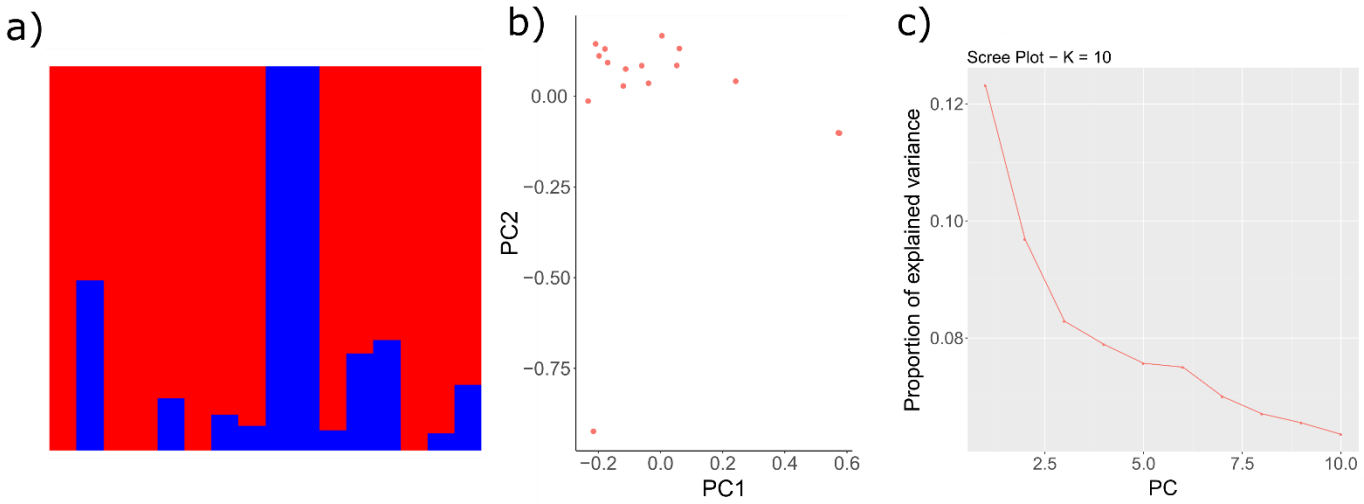


Fig.S5.5 Genetic structure within KNU-L based on N = 7378 SNPs. a) ADMIXTURE plot for K = 2, b) PCA, c) Scree Plot of the proportion of genetic variance explained by each PC.

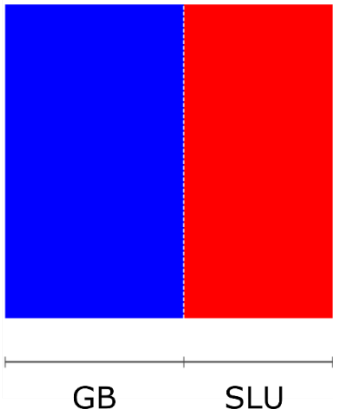


Fig.S5.6 ADMIXTURE plot for K = 2 within Voisey Bay landlocked lakes GB-L and SLU-L based on N = 13886 SNPs.

Table S5.3 Maturity, sex, and glacial lineage information for samples from landlocked lakes with no evidence based on ADMIXTURE of genetic sub-structuring.

Location	N	Immature Males	Immature Females	Mature Males	Mature Females	Atlantic Lineage	Arctic Lineage	Acadian Lineage
HEB-L	30	5	11	11	3	24	0	0
BS-L	29	7	7	8	7	0	20	0
KNU-L	16					0	0	16
SLU-L	10					5	5	0
GB-L	12					12	0	0

Table S5.4 The number of outlier loci which were detected by each outlier detection method between small (s) and big (b) morphs within each of WP-L and LO-L.

Outlier Detection Method	sWP-L vs. bWP-L	sLO-L vs. bLO-L
Both PCAdapt and F_{ST}	57	269
PCAdapt Only	4	87
F_{ST} Only	47	44
Total	108	400

Table S5.5 The number of outlier and non-outlier SNPs detected between morphs (small and big) within a given lake that were found to be polymorphic outliers, polymorphic non-outliers or non-polymorphic in each of WP-L and LO-L.

	WP-L (N = 6404)		LO-L (N = 16702)	
	Outlier (N = 108)	Non-outlier (N = 6296)	Outlier (N = 400)	Non-outlier (N = 16302)
WP-L Polymorphic Outlier	108	0	1	95
WP-L Polymorphic Non-outlier	0	6296	135	5952
WP-L Non-polymorphic	0	0	264	10255
LO-L Polymorphic Outlier	1	135	400	0
LO-L Polymorphic Non-outlier	95	5952	0	16302
LO-L Non-polymorphic	12	209	0	0

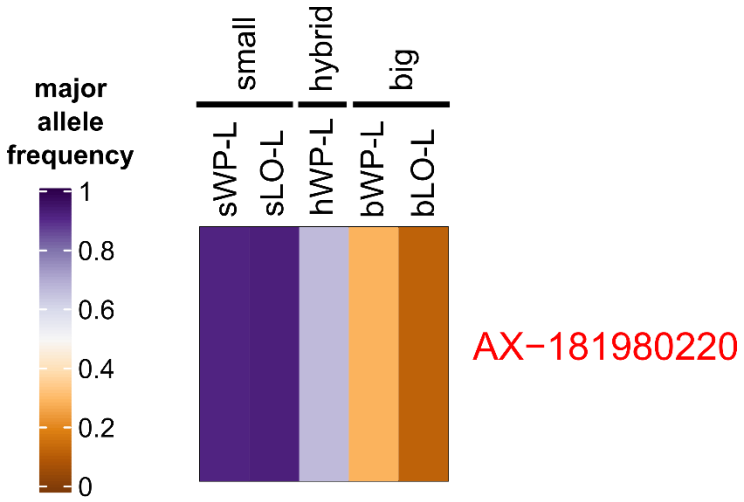


Fig.S5.7 Heatmap of allele frequencies of loci detected as outliers within both WP-L and LO-L. The names of SNPs which show parallel allelic trends across locations are highlighted in red.

Table S5.6 Genes containing outlier loci differentiating sympatric small (s) and big (b) morphs within both WP-L and LO-L. The method by which each SNP was identified as an outlier is denoted for each comparison between morphs within each lake (P – PCAdapt, F- F_{ST}).

						Method by which outlier was detected	
Gene Name	**Linkage Group**	**Protein Code**	**SNP Code**	**Position (bp)**	**Position Relative to CDS (bp)**	**sWP-L vs. bWP-L**	**sLO-L vs. bLO-L**
VPS10 domain-containing receptor SorCS2	AC37	XP_023837960.1	AX-181980220	14860156	0	P,F	F
	AC37	XP_023837960.1	AX-181940385	14881202	0	F	
	AC37	XP_023837960.1	AX-181940384	14881248	0	F	

Table S5.7 Paralogous genes containing outlier loci differentiating sympatric small and big morphs in LO-L. For a given gene, starred linkage groups are homeologous.

Lake	General Gene Name	Linkage Group	Protein Code	Specific Gene Name	SNP Code	Position (bp)	Position relative to CDS (bp)
LO-L	cell adhesion molecule 1	AC04p	XP_023835529.1	cell adhesion molecule 1-like isoform X2	AX-181952039	1159420	0
		AC04p	XP_023835529.1	cell adhesion molecule 1-like isoform X2	AX-181952040	1222264	0
		AC23	XP_023824730.1	cell adhesion molecule 1-like	AX-181971323	16203550	0
		AC23	XP_023824730.1	cell adhesion molecule 1-like	AX-181971324	16397382	0
LO-L	ras-interacting protein 1	AC06.1	XP_023844435.1	ras-interacting protein 1	AX-181978405	1025171	0
		AC06.1	XP_023844436.1	ras-interacting protein 1	AX-181942587	1068760	0

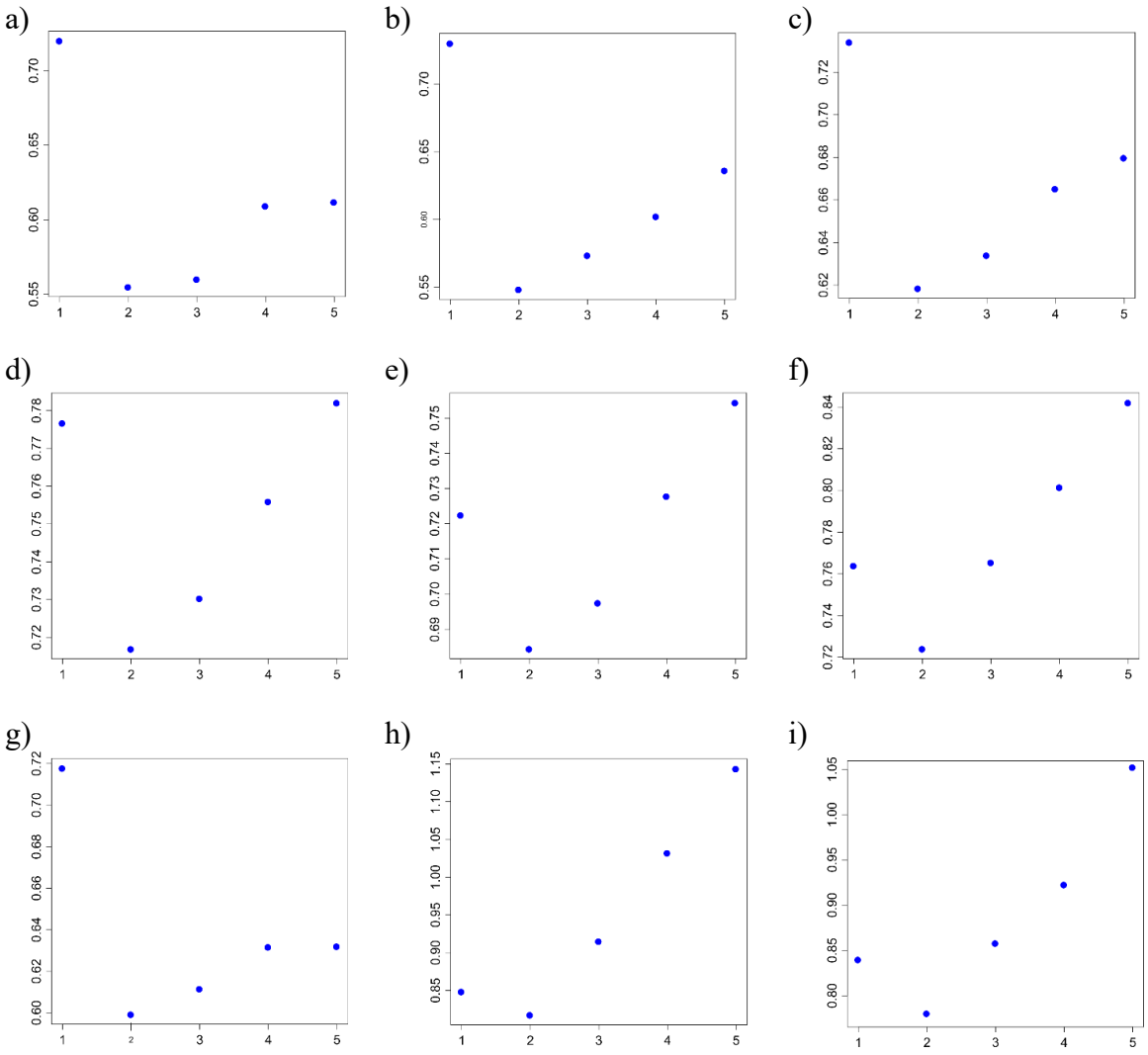


Fig.S5.8 SNMF cross-entropy values vs K-values for 9 landlocked vs. anadromous population comparisons: a) sWP-L vs. SWA-A, b) bWP-L vs. SWA-A, c) HEB-L vs. IKA-A, d) BS-L vs. K05-A, e) sLO-L vs. K05-A, f) bLO-L vs. K05-A, g) KNU-L vs. ANA-A, h) SLU-L vs. REI-A, i) GB-L vs. REI-A.

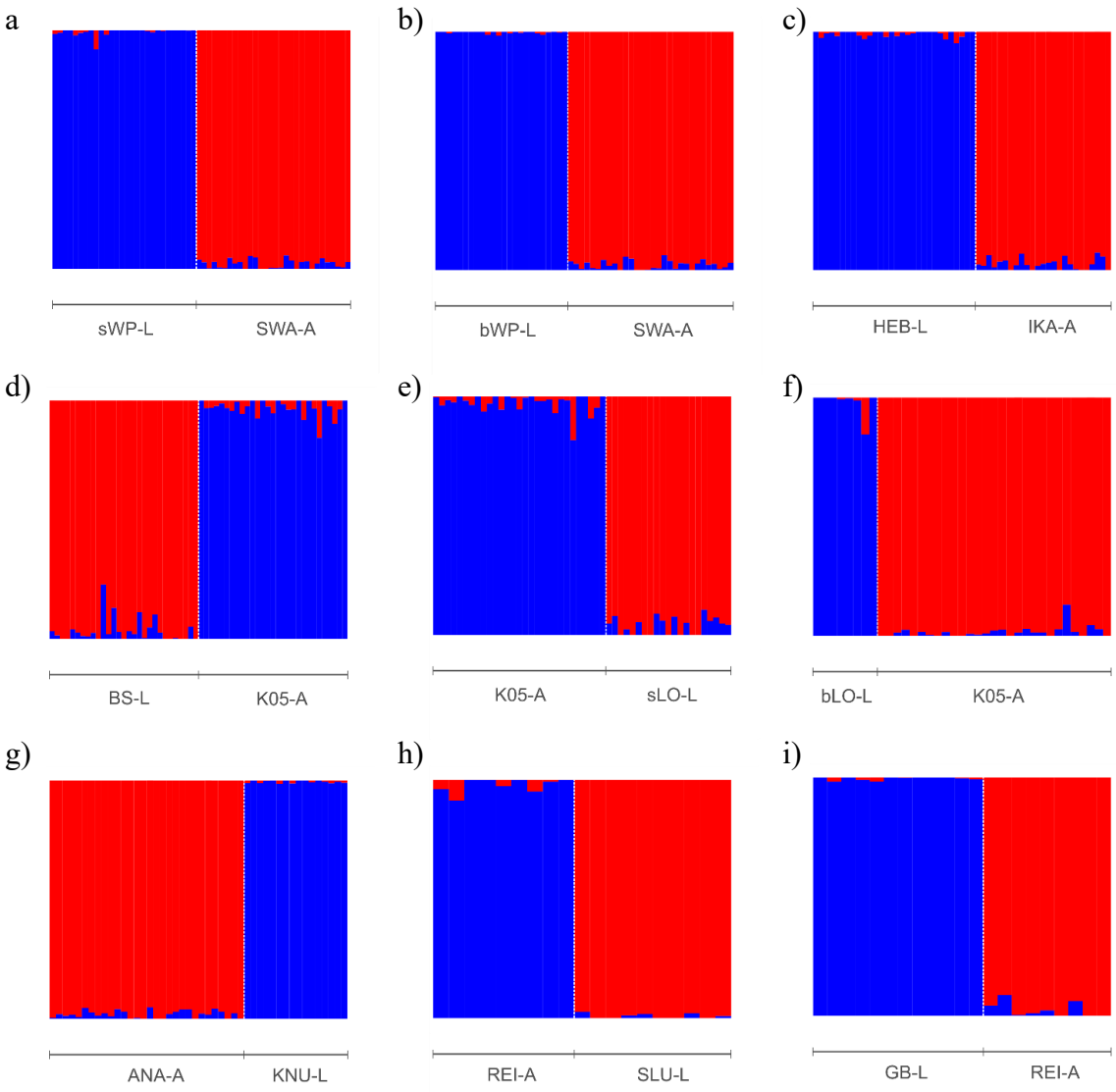


Fig.S5.9 SNMF plots for K = 2 for 9 landlocked vs. anadromous population comparisons: a) sWP-L vs. SWA-A, b) bWP-L vs. SWA-A, c) HEB-L vs. IKA-A, d) BS-L vs. K05-A, e) sLO-L vs. K05-A, f) bLO-L vs. K05-A, g) KNU-L vs. ANA-A, h) SLU-L vs. REI-A, i) GB-L vs. REI-A.

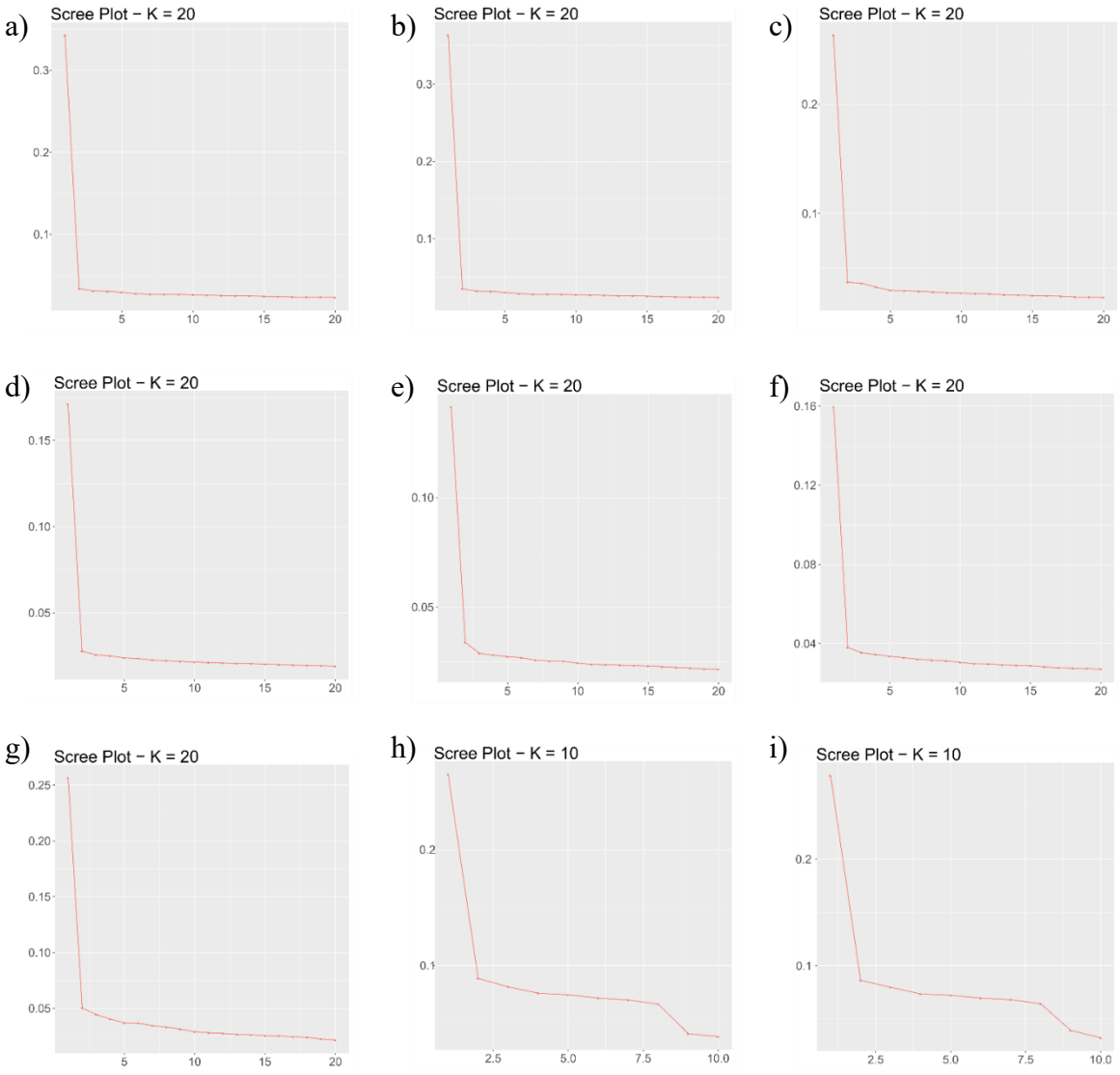


Fig.S5.10 Proportion of explained variance vs PC of PCAdapt population structure analysis for a) sWP-L vs. SWA-A, b) bWP-L vs. SWA-A, c) HEB-L vs. IKA-A, d) BS-L vs. K05-A, e) sLO-L vs. K05-A, f) bLO-L vs. K05-A, g) KNU-L vs. ANA-A, h) SLU-L vs. REI-A, i) GB-L vs. REI-A.

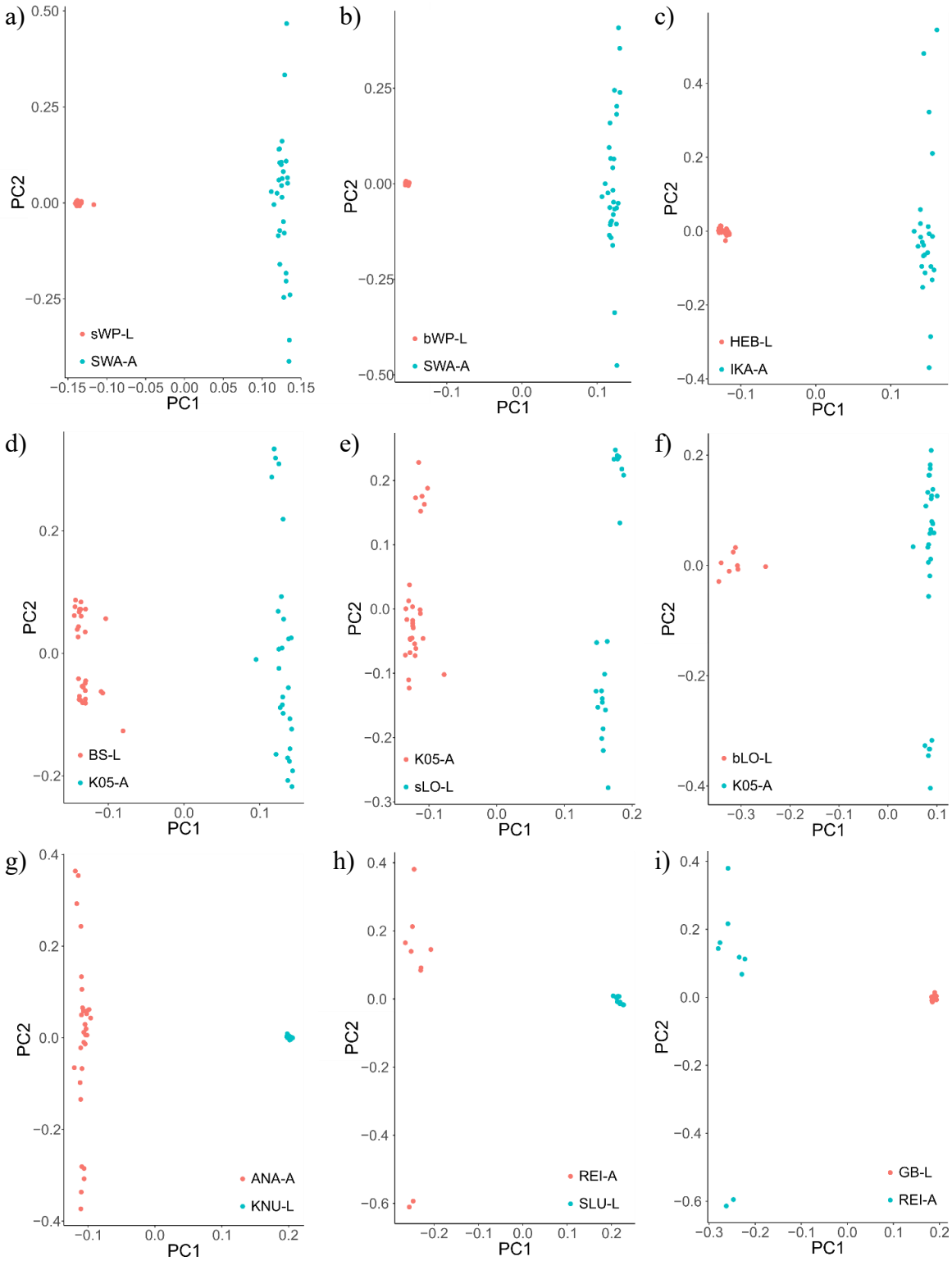


Fig.S5.11 PCAdapt plots for a) sWP-L vs. SWA-A, b) bWP-L vs. SWA-A, c) HEB-L vs. IKA-A, d) BS-L vs. K05-A, e) sLO-L vs. K05-A, f) bLO-L vs. K05-A, g) KNU-L vs. ANA-A, h) SLU-L vs. REI-A, i) GB-L vs. REI-A.

Table S5.8 Number of SNPs, pairwise F_{ST} values, number of outlier SNPs and associated linkage groups in nine comparisons of landlocked and anadromous populations paired by drainage.

Drainage	Locations Compared	N SNPs	Mean Pairwise F_{ST}	Weighted Pairwise F_{ST}	N Outlier SNPs	N Linkage groups containing outlier SNPs
Saglek	sWP-L vs. SWA-A	20393	0.242348	0.358117	1616	39
Saglek	bWP-L vs. SWA-A	20361	0.256677	0.38625	1366	39
Hebron	HEB-L vs. IKA-A	19613	0.191969	0.254762	548	39
Okak	BS-L vs. K05-A	20334	0.12467	0.168579	370	35
Okak	sLO-L vs. K05-A	22540	0.100295	0.151193	465	38
Okak	bLO-L vs. K05-A	22185	0.130439	0.220815	2250	39
Anaktalik	KNU-L vs. ANA-A	19994	0.187325	0.317178	2296	39
Voisey	SLU-L vs. REI-A	17385	0.155127	0.230577	546	37
Voisey	GB-L vs. REI-A	17321	0.17172	0.247372	479	38

Table S5.9 The number of outlier SNPs which were detected by each outlier detection method within each of nine comparisons of landlocked and anadromous populations.

Outlier Detection Method	sWP-L vs. SWA-A	bWP-L vs. SWA-A	HEB-L vs. IKA-A	BS-L vs. K05-A	sLO-L vs. K05-A	bLO-L vs. K05-A	KNU-L vs. ANA-A	SLU-L vs. REI-A	GB-L vs. REI-A
PCAdapt and F_{ST}	74	67	201	152	270	393	213	277	168
PCAdapt Only	1542	1299	345	14	13	1857	2083	263	300
F_{ST} Only	0	0	2	204	182	0	0	6	11
Total	1616	1366	548	370	465	2250	2296	546	479

Table S5.10 The number of outlier and non-outlier SNPs detected between landlocked and anadromous populations that were found to be polymorphic outliers, polymorphic non-outliers or non-polymorphic in each of the landlocked vs. anadromous population comparisons.

	sWP-L vs. SWA-A (N=20393)		bWP-L vs. SWA-A (N=20361)		HEB-L vs. IKA-A (N=19613)		BS-L vs. K05-A (N=20334)		sLO-L vs. K05-A (N=22540)		bLO-L vs. K05-A (N=22185)		KNU-L vs. ANA-A (N=19994)		SLU-L vs. REI-A (N=17385)		GB-L vs. REI-A (N=17321)	
	Outlier (N=1616)	Non-Outlier (N=18777)	Outlier (N=1366)	Non-Outlier (N=18995)	Outlier (N=548)	Non-Outlier (N=19065)	Outlier (N=370)	Non-Outlier (N=19964)	Outlier (N=465)	Non-Outlier (N=22075)	Outlier (N=2250)	Non-Outlier (N=19935)	Outlier (N=2296)	Non-Outlier (N=17698)	Outlier (N=546)	Non-Outlier (N=16839)	Outlier (N=479)	Non-Outlier (N=16842)
sWP-L vs. SWA-A Polymorphic Outlier	1616	0	988	622	76	1455	58	1515	103	1485	339	1234	384	1192	84	1463	67	1430
sWP-L vs. SWA-A Polymorphic Non-Outlier	0	18777	376	18359	436	16483	296	16148	329	16932	1617	15580	1859	14627	448	14375	400	14365
sWP-L vs. SWA-A Non-polymorphic	0	0	2	14	36	1127	16	2301	33	3658	294	3121	53	1879	14	1001	12	1047
bWP-L vs. SWA-A Polymorphic Outlier	988	376	1366	0	70	1214	53	1289	89	1265	327	1016	361	976	76	1203	49	1214
bWP-L vs. SWA-A Polymorphic Non-Outlier	622	18359	0	18995	438	16707	301	16348	343	17123	1623	15777	1880	14820	454	14615	417	14567
bWP-L vs. SWA-A Non-polymorphic	6	42	0	0	40	1144	16	2327	33	3687	300	3142	55	1902	16	1021	13	1061
HEB-L vs. IKA-A Polymorphic Outlier	76	436	70	438	548	0	33	475	27	498	89	433	106	410	27	446	21	443
HEB-L vs. IKA-A Polymorphic Non-Outlier	1455	16483	1214	16707	0	19065	314	16899	398	17565	1815	16097	2106	15037	494	15132	434	15155
HEB-L vs. IKA-A Non-polymorphic	85	1858	82	1850	0	0	23	2590	40	4012	346	3405	84	2251	25	1261	24	1244
BS-L vs. K05-A Polymorphic Outlier	58	296	53	301	33	314	370	0	118	252	188	182	104	247	39	299	34	302
BS-L vs. K05-A Polymorphic Non-Outlier	1515	16148	1289	16348	475	16899	0	19964	344	19492	1861	17920	2144	15547	503	15584	436	15594
BS-L vs. K05-A Non-polymorphic	43	2333	24	2346	40	1852	0	0	3	2331	201	1833	48	1904	4	956	9	946
sLO-L vs. K05-A Polymorphic Outlier	103	329	89	343	27	398	118	344	465	0	261	202	145	286	38	380	36	372
sLO-L vs. K05-A Polymorphic Non-Outlier	1485	16932	1265	17123	498	17565	252	19492	0	22075	1953	19617	2119	16122	502	15839	438	15857
sLO-L vs. K05-A Non-polymorphic	28	1516	12	1529	23	1102	0	128	0	0	36	116	32	1290	6	620	5	613
bLO-L vs. K05-A Polymorphic Outlier	339	1617	327	1623	89	1815	188	1861	261	1953	2250	0	405	1556	103	1734	81	1722
bLO-L vs. K05-A Polymorphic Non-Outlier	1234	15580	1016	15777	433	16097	182	17920	202	19617	0	19935	1853	14789	434	14431	393	14456
bLO-L vs. K05-A Non-polymorphic	43	1580	23	1595	26	1153	0	183	2	505	0	0	38	1353	9	674	5	664
KNU-L vs. ANA-A Polymorphic Outlier	384	1859	361	1880	106	2106	104	2144	145	2119	405	1853	2296	0	166	2042	135	2049
KNU-L vs. ANA-A Polymorphic Non-Outlier	1192	14627	976	14820	410	15037	247	15547	286	16122	1556	14789	0	17698	370	13986	335	13996
KNU-L vs. ANA-A Non-polymorphic	40	2291	29	2295	32	1922	19	2273	34	3834	289	3293	0	0	10	811	9	797
SLU-L vs. REI-A Polymorphic Outlier	84	448	76	454	27	494	39	503	38	502	103	434	166	370	546	0	159	374
SLU-L vs. REI-A Polymorphic Non-Outlier	1463	14375	1203	14615	446	15132	299	15584	380	15839	1734	14431	2042	13986	0	16839	311	15938
SLU-L vs. REI-A Non-polymorphic	69	3954	87	3926	75	3439	32	3877	47	5734	413	5070	88	3342	0	0	9	530
GB-L vs. REI-A Polymorphic Outlier	67	400	49	417	21	434	34	436	36	438	81	393	135	335	159	311	479	0
GB-L vs. REI-A Polymorphic Non-Outlier	1430	14365	1214	14567	443	15155	302	15594	372	15857	1722	14456	2049	13996	374	15938	0	16842
GB-L vs. REI-A Non-polymorphic	119	4012	103	4011	84	3476	34	3934	57	5780	447	5086	112	3367	13	590	0	0

Table S5.11 Top Biological Processes GO terms with an unadjusted p-value < 0.01 for outlier loci within at least five of seven paired landlocked and anadromous populations (1) WP-L vs. SWA-A (either sWP-L vs. SWA-A or bWP-L vs. SWA-A), 2) HEB-L vs. IKA-A, 3) BS-L vs. K05-A, 4) LO-L vs. K05-A (either sLO-L vs. K05-A or bLO-L vs. K05-A), 5) KNU-L vs. ANA-A, 6) SLU-L vs. REI-A, 7) GB-L vs. REI-A).

GO.ID	Term	Annotated	Significant	Expected	weight01	weight01padj
GO:0010390	histone monoubiquitination	25	2	0.07	0.0022	1
GO:1903259	exon-exon junction complex disassembly	1	1	0	0.0028	1
GO:0031399	regulation of protein modification proce...	1529	5	4.33	0.0054	1
GO:0034402	recruitment of 3'-end processing factors...	2	1	0.01	0.0057	1
GO:1990091	sodium-dependent self proteolysis	2	1	0.01	0.0057	1
GO:0018022	peptidyl-lysine methylation	97	2	0.27	0.0082	1
GO:2001168	positive regulation of histone H2B ubiqu...	3	1	0.01	0.0085	1
GO:0006807	nitrogen compound metabolic process	4998	18	14.14	0.009	1

Table S5.12 Genes for which different paralogous outlier loci were detected in different landlocked vs. anadromous population comparisons for five or more of seven comparisons (1) WP-L vs. SWA-A (either sWP-L vs. SWA-A or bWP-L vs. SWA-A), 2) HEB-L vs. IKA-A, 3) BS-L vs. K05-A, 4) LO-L vs. K05-A (either sLO-L vs. K05-A or bLO-L vs. K05-A), 5) KNU-L vs. ANA-A, 6) SLU-L vs. REI-A, 7) GB-L vs. REI-A). The method by which each SNP was identified as an outlier is denoted for each landlocked vs. anadromous population comparison (P – PCAdapt, F- F_{ST}). For a given gene, starred linkage groups are homeologous.

							Method by which outlier was detected								
General Gene Name	Linkage Group	Protein Code	Specific Gene Name	SNP Code	Absolute location (bp)	Relative location (bp)	sWP-L vs. SWA-A	bWP-L vs. SWA-A	HEB-L vs. IKA-A	BS-L vs. K05-A	sLO-L vs. K05-A	bLO-L vs. K05-A	KNU-L vs. ANA-A	SLU-L vs. REI-A	GB-L vs. REI-A
adhesion G-protein coupled receptor G2	AC06.2	XP_023845604.1	adhesion G-protein coupled receptor G2-like	AX-181975480	1903649	0						P			
	AC06.2	XP_023845604.1	adhesion G-protein coupled receptor G2-like	AX-181929714	1917027	0				F					
	AC14	XP_023856439.1	adhesion G-protein coupled receptor G2 isoform X2	AX-181935811	3853463	0			P					P	
	AC14	XP_023856439.1	adhesion G-protein coupled receptor G2 isoform X2	AX-181964222	3860715	0						P			
	AC23	XP_023824679.1	adhesion G-protein coupled receptor G2	AX-181963321	39484542	1285	P	P							
chloride channel protein 2	AC04p	XP_023838719.1	LOW QUALITY PROTEIN: chloride channel protein 2-like	AX-181945304	25009913	0	P							P	
	AC32	XP_023833454.1	chloride channel protein 2-like	AX-181978855	14359293	0	P	P	P			P	P		
E3 ubiquitin-protein ligase BRE1B	AC17	XP_023860736.1	E3 ubiquitin-protein ligase BRE1B	AX-181928576	37402070	0		P							
	AC18	XP_023862569.1	E3 ubiquitin-protein ligase BRE1B isoform X2	AX-181935230	13010818	0			P,F	P,F	P,F		P		P
	AC18	XP_023862569.1	E3 ubiquitin-protein ligase BRE1B isoform X2	AX-181935231	13016862	0			P,F	P,F	P,F		P		
ephrin type-A receptor 3	AC02	XP_023863833.1	ephrin type-A receptor 3	AX-181971250	32111599	0						P			
	AC02	XP_023863833.1	ephrin type-A receptor 3	AX-181971249	32181057	0						P			
	AC02	XP_023863833.1	ephrin type-A receptor 3	AX-181971248	32243255	0		P				P			
	AC02	XP_023863833.1	ephrin type-A receptor 3	AX-181944140	32486740	0							P		
	NW_019942998.1	XP_023994522.1	LOW QUALITY PROTEIN: ephrin type-A receptor 3-like	AX-181991583	168029	0								P,F	P,F
extended synaptotagmin-1	AC01*	XP_023846266.1	extended synaptotagmin-1 isoform X1	AX-181925736	33686150	0	P	P					P,F		
	AC01*	XP_023846266.1	extended synaptotagmin-1 isoform X1	AX-181930078	33693553	0	P	P					P		
	AC11*	XP_023852472.2	extended synaptotagmin-1	AX-181939957	30693817	0			P	P,F	P,F	P,F	P	P,F	

Table S5.12 Continued.

General Gene Name	Linkage Group	Protein Code	Specific Gene Name	SNP Code	Absolute location (bp)	Relative location (bp)	Method by which outlier was detected								
							sWP-L vs. SWA-A	bWP-L vs. SWA-A	HEB-L vs. IKA-A	BS-L vs. K05-A	sLO-L vs. K05-A	bLO-L vs. K05-A	KNU-L vs. ANA-A	SLU-L vs. REI-A	GB-L vs. REI-A
gastrula zinc finger protein XlCGF57.1	AC06.1	XP_024002901.1	gastrula zinc finger protein XlCGF57.1 isoform X4	AX-181942043	1491293	352		P		P,F	P,F	P,F			P
	AC14	XP_023856467.1	gastrula zinc finger protein XlCGF57.1-like	AX-181937152	3664878	0						P	P		
	AC14	XP_023856467.1	gastrula zinc finger protein XlCGF57.1-like	AX-181937150	3665111	0							P		
homeobox protein MSX-2	AC23	XP_023824809.1	homeobox protein MSX-2	AX-181967650	3204274	0	P	P			P		P		
	NW_019943350.1	XP_023995838.1	homeobox protein MSX-2-like isoform X1	AX-181920182	147629	-493			P,F	F					
neurexin-3a	AC04q.2	XP_023842075.1	neurexin-3a-like	AX-181947935	28835631	0								P,F	
	AC04q.2	XP_023842075.1	neurexin-3a-like	AX-181915470	28938899	0	P		P		F	P	P		
	AC04q.2	XP_023842075.1	neurexin-3a-like	AX-181937420	29244795	0	P	P							
	NW_019942794.1	XP_023993341.1	neurexin-3a-like	AX-181941664	132331	-2625							P		
neuronal PAS domain-containing protein 3	AC04q.2	XP_023841991.1	LOW QUALITY PROTEIN: neuronal PAS domain-containing protein 3-like	AX-181915280	20947834	0								P,F	P
	AC05	XP_023844009.1	neuronal PAS domain-containing protein 3	AX-181952675	32673429	-172	P	P				P,F	P		
PAN2-PAN3 deadenylation complex catalytic subunit PAN2	AC07*	XP_023847330.1	PAN2-PAN3 deadenylation complex catalytic subunit PAN2	AX-181977426	25038612	0						P			
	AC07*	XP_023847330.1	PAN2-PAN3 deadenylation complex catalytic subunit PAN2	AX-181935260	25047954	0						P			
	AC17*	XP_023861482.1	PAN2-PAN3 deadenylation complex catalytic subunit PAN2 isoform X1	AX-181952107	22685483	-2559				P,F	P,F	P,F	P,F	P	P,F
parafibromin	AC19*	XP_023865178.1	parafibromin	AX-181969955	34116352	0	P	P	P,F	P	F		P		
	AC32*	XP_023833739.1	parafibromin	AX-181942618	7899572	0			P						
	AC32*	XP_023833739.1	parafibromin	AX-181934703	7907469	0			P,F			P			
piezo-type mechanosensitive ion channel component 2	AC27	XP_023829138.1	piezo-type mechanosensitive ion channel component 2-like	AX-181930959	6916977	0							P		
	NW_019944187.1	XP_023997787.1	LOW QUALITY PROTEIN: piezo-type mechanosensitive ion channel component 2-like	AX-181973456	68105	0			P	P,F		P		P	

Table S5.12 Continued.

General Gene Name	Linkage Group	Protein Code	Specific Gene Name	SNP Code	Absolute location (bp)	Relative location (bp)	Method by which outlier was detected								
							sWP-L vs. SWA-A	bWP-L vs. SWA-A	HEB-L vs. IKA-A	BS-L vs. K05-A	sLO-L vs. K05-A	bLO-L vs. K05-A	KNU-L vs. ANA-A	SLU-L vs. REI-A	GB-L vs. REI-A
pro-neuregulin-3, membrane-bound	AC17	XP_023860894.1	pro-neuregulin-3, membrane-bound isoform-like	AX-181941701	38644082	0						P			
	AC17	XP_023860894.1	pro-neuregulin-3, membrane-bound isoform-like	AX-181922212	38683416	0						P			
	AC17	XP_023860894.1	pro-neuregulin-3, membrane-bound isoform-like	AX-181942722	38714491	0			P						
	AC17	XP_023860894.1	pro-neuregulin-3, membrane-bound isoform-like	AX-181913589	38714498	0						P			
	AC17	XP_023860894.1	pro-neuregulin-3, membrane-bound isoform-like	AX-181974022	38788922	0						P			
	AC17	XP_023860894.1	pro-neuregulin-3, membrane-bound isoform-like	AX-181914524	39021739	0	P								
	AC18*	XP_023864068.1	pro-neuregulin-3, membrane-bound isoform	AX-181914283	21240882	0						P	P		
	AC18*	XP_023864068.1	pro-neuregulin-3, membrane-bound isoform	AX-181942151	21541076	0		P				P	P		
	AC18*	XP_023864284.1	pro-neuregulin-3, membrane-bound isoform-like	AX-181943495	43996520	0	P								
	AC25*	XP_023825564.1	pro-neuregulin-3, membrane-bound isoform isoform X2	AX-181942348	20692272	0								P	
protocadherin-11 X-linked	AC08	XP_023847824.1	LOW QUALITY PROTEIN: protocadherin-11 X-linked-like	AX-181937960	798438	0	P	P				P	P	P	P,F
	NW_019942572.1	XP_023991446.1	protocadherin-11 X-linked-like	AX-181957245	792874	-4374	P	P	P,F			P			
type I inositol 1,4,5-trisphosphate 5-phosphatase	AC18*	XP_023863329.1	type I inositol 1,4,5-trisphosphate 5-phosphatase isoform X2	AX-181926142	29494356	0	P	P			P,F	P			
	AC18*	XP_023863329.1	type I inositol 1,4,5-trisphosphate 5-phosphatase isoform X2	AX-181948291	29497976	0							P		P,F
	AC25*	XP_023825797.1	type I inositol 1,4,5-trisphosphate 5-phosphatase-like isoform X2	AX-181939239	7727750	0						P		P	
sialic acid-binding Ig	AC06.1	XP_023844980.1	sialic acid-binding Ig-like lectin 5	AX-181937410	15048474	0	P	P					P,F	P,F	P,F
	AC35	XP_023836226.1	sialic acid-binding Ig-like lectin 5	AX-181935420	11660641	0						P			

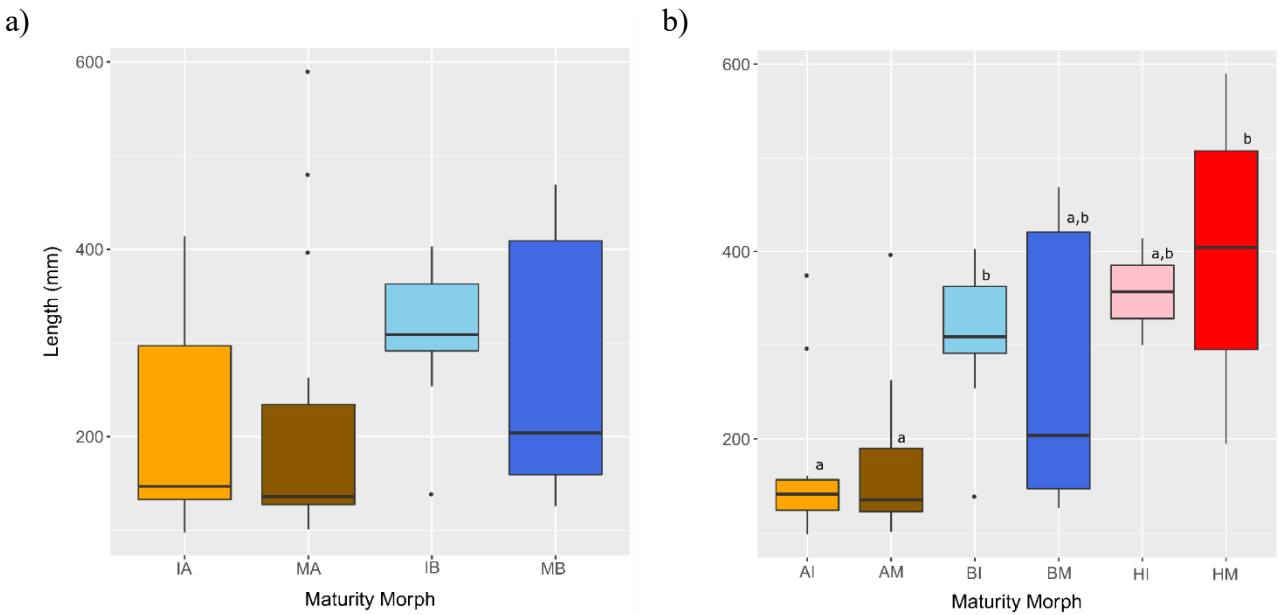


Fig.S5.12 Boxplots demonstrating length of fish by maturity (immature (I), mature (M)) and assigned genetic group (A or B, as assigned based on 11 microsatellites in Salisbury et al. 2018) in WP-L a) before and b) after separating individuals assigned as putative hybrids (H) detected using 6404 SNPs in this study. Lengths of the WP individuals used in this study were compared according to maturity status (N=55, as three samples had unknown maturity status), and their genetic group as assigned using microsatellites by Salisbury et al. (2018). A 2-way ANOVA testing the interaction of microsatellite-assigned genetic group and maturity found marginally significant differences in length between genetic groups ($F_{1,51} = 6.819$, $p > 0.01$). However, no significant pairwise Tukey HSD test results were observed between any pairwise comparisons among maturity/genetic groups (all $p > 0.05$) (Fig. S5.12a). However, after separating the six individuals identified as hybrids based on our SNP analysis, more significant differences in length were observed among the microsatellite-assigned genetic groups (1-way ANOVA testing for differences in lengths among six groups varying in maturity, SNP-assigned hybrid status, and microsatellite-assigned genetic group: $F_{5,49} = 6.213$, $p < 0.001$) (Fig. S5.12b). Shared letters among boxplots in Fig. S5.12b indicate a lack of statistical difference ($\alpha = 0.05$) after a Tukey HSD test. Therefore, the lack of size differences observed between genetically distinguishable morphs in Salisbury et al. (2018) was potentially due to the failure to remove putative hybrid individuals. Further discrepancies in morph assignment between our SNP data and the microsatellite data may be due to greater assignment accuracy with 6404 SNPs in comparison to 11 microsatellites.

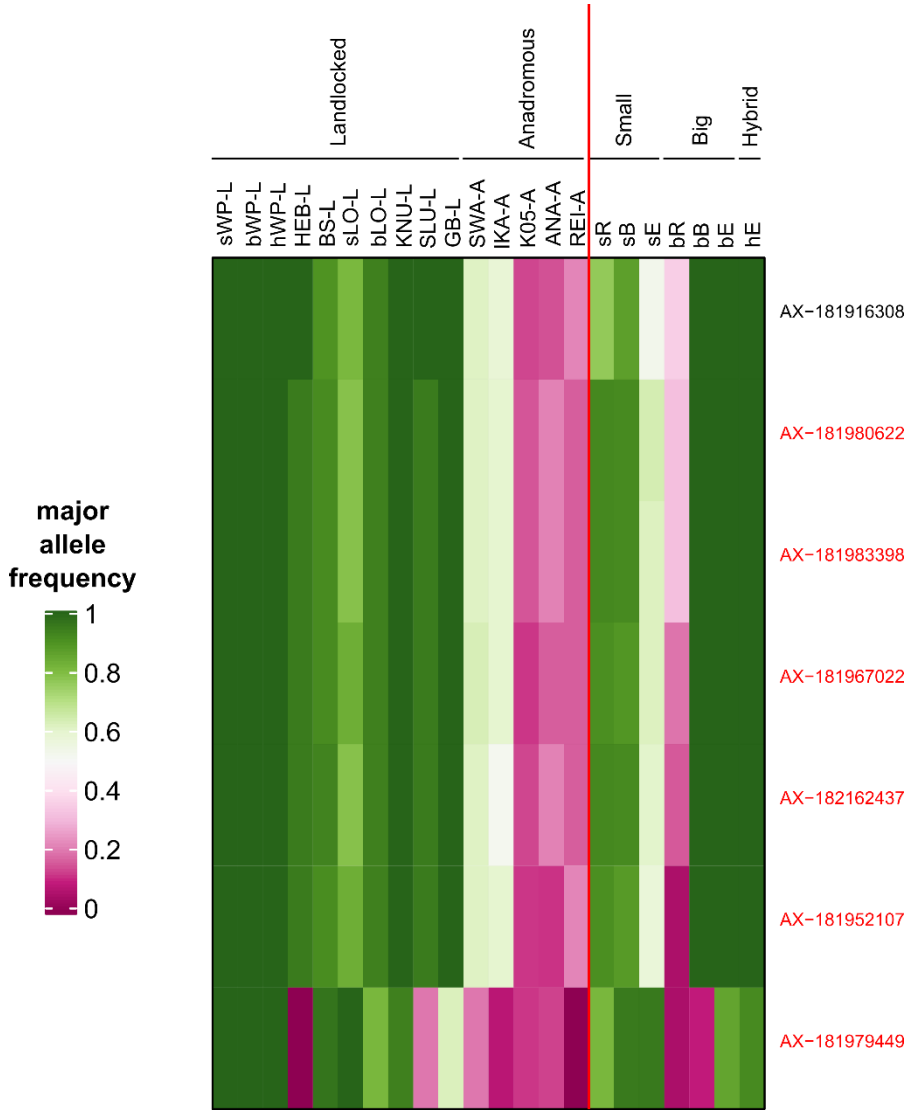


Fig.S5.13 Heatmap of allele frequencies for those SNPs detected as outliers for five or more of seven paired landlocked and anadromous populations (1) WP-L vs. SWA-A (either sWP-L vs. SWA-A or bWP-L vs. SWA-A), 2) HEB-L vs. IKA-A, 3) BS-L vs. K05-A, 4) LO-L vs. K05-A (either sLO-L vs. K05-A or bLO-L vs.K05-A), 5) KNU-L vs. ANA-A, 6) SLU-L vs. REI-A, 7) GB-L vs. REI-A) and at least one location with sympatric small (s), and big (b morphs from Salisbury et al. (2020). The names of SNPs which show parallel allelic trends across the locations in which a SNP was detected as an outlier are highlighted in red.

Table S5.13 SNPs detected as outliers for five or more of seven paired landlocked and anadromous populations (1) WP-L vs. SWA-A (either sWP-L vs. SWA-A or bWP-L vs. SWA-A), 2) HEB-L vs. IKA-A, 3) BS-L vs. K05-A, 4) LO-L vs. K05-A (either sLO-L vs. K05-A or bLO-L vs.K05-A), 5) KNU-L vs. ANA-A, 6) SLU-L vs. REI-A, 7) GB-L vs. REI-A) and at least one location with sympatric small (s), and big (b), morphs from Salisbury et al. (2020).

						Landlocked vs. Anadromous									Small vs. Big		
General Gene Name	Linkage Group	Protein Code	SNP Code	Position (bp)	Position Relative to CDS (bp)	sWP-L vs. SWA-A	bWP-L vs. SWA-A	HEB-L vs. IKA-A	BS-L vs. K05-A	sLO-L vs. K05-A	bLO-L vs. K05-A	KNU-L vs. ANA-A	SLU-L vs. REI-A	GB-L vs. REI-A	sR vs. bR	sB vs. bB	sE vs. bE
NA	AC13	NA	AX-181979449	27246077	NA	*	*		*	*	*	*		*	*	*	
partner of Y14 and mago B	AC17	XP_023861958.1	AX-181916308	22616133	98				*	*	*	*	*	*			*
PAN2-PAN3 deadenylation complex catalytic subunit PAN2 isoform X1	AC17	XP_023861482.1	AX-181952107	22685483	-2559				*	*	*	*	*	*	*		
nuclear envelope integral membrane protein 1-like isoform X1	AC17	XP_023862374.1	AX-181967022	22704350	0				*	*	*	*	*	*	*		
LOW QUALITY PROTEIN: serine/threonine-protein phosphatase 6 regulatory ankyrin repeat subunit C-like	AC17	XP_023862177.1	AX-181980622	22869580	2738				*	*	*	*	*	*	*		
			AX-181983398	22869600	2718				*	*	*	*	*	*	*		
inactive dipeptidyl peptidase 10	AC17	XP_023860785.1	AX-182162437	22923504	0				*	*	*	*	*	*	*		

Table S5.14 Genes for which different paralogous outlier loci were detected in different landlocked vs. anadromous population comparisons for five or more of seven comparisons (1) WP-L vs. SWA-A (either sWP-L vs. SWA-A or bWP-L vs. SWA-A), 2) HEB-L vs. IKA-A, 3) BS-L vs. K05-A, 4) LO-L vs. K05-A (either sLO-L vs. K05-A or bLO-L vs. K05-A), 5) KNU-L vs. ANA-A, 6) SLU-L vs. REI-A, 7) GB-L vs. REI-A) and at least one location with sympatric small (s), and big (b), morphs from Salisbury et al. (2020). For a given gene, starred linkage groups are homeologous.

							Landlocked vs. Anadromous									Small vs. Big		
General Gene Name	Linkage Group	Protein Code	Specific Gene Name	SNP Code	Position (bp)	Position Relative to CDS (bp)	sWP-L vs. SWA-A	bWP-L vs. SWA-A	HEB-L vs. IKA-A	BS-L vs. K05-A	sLO-L vs. K05-A	bLO-L vs. K05-A	KNU-L vs. ANA-A	SLU-L vs. REI-A	GB-L vs. REI-A	sR vs. bR	sB vs. bB	sE vs. bE
neurexin-3a	AC04q.2*	XP_023842075.1	neurexin-3a-like	AX-181947935	28835631	0								*				
	AC04q.2*	XP_023842075.1	neurexin-3a-like	AX-181915470	28938899	0	*		*		*	*	*					
	AC04q.2*	XP_023842075.1	neurexin-3a-like	AX-181937420	29244795	0	*	*										
	AC09*	XP_023849683.1	neurexin-3a isoform X8	AX-181915852	1569280	0										*		
	NW_019942794.1	XP_023993341.1	neurexin-3a-like	AX-181941664	132331	-2625							*					
neuronal PAS domain-containing protein 3	AC04q.2	XP_023841991.1	LOW QUALITY PROTEIN: neuronal PAS domain-containing protein 3-like	AX-181915280	20947834	0								*	*			
	AC05	XP_023844009.1	neuronal PAS domain-containing protein 3	AX-181952675	32673429	-172	*	*				*	*					*
PAN2-PAN3 deadenylation complex catalytic subunit PAN2	AC07*	XP_023847330.1	PAN2-PAN3 deadenylation complex catalytic subunit PAN2	AX-181977426	25038612	0						*						*
	AC07*	XP_023847330.1	PAN2-PAN3 deadenylation complex catalytic subunit PAN2	AX-181935260	25047954	0						*						*
	AC17*	XP_023861482.1	PAN2-PAN3 deadenylation complex catalytic subunit PAN2 isoform X1	AX-181952107	22685483	-2559				*	*	*	*	*	*	*		

Table S5.14 Continued.

General Gene Name	Linkage Group	Protein Code	Specific Gene Name	SNP Code	Position (bp)	Position Relative to CDS (bp)	Landlocked vs. Anadromous								Small vs. Big		
							sWP-L vs. SWA-A	bWP-L vs. SWA-A	HEB-L vs. IKA-A	BS-L vs. K05-A	sLO-L vs. K05-A	bLO-L vs. K05-A	KNU-L vs. ANA-A	SLU-L vs. REI-A	GB-L vs. REI-A	sR vs. bR	sB vs. bB	sE vs. bE
pro-neuregulin-3, membrane-bound	AC17	XP_023860894.1	pro-neuregulin-3, membrane-bound isoform-like	AX-181941701	38644082	0						*				*		
	AC17	XP_023860894.1	pro-neuregulin-3, membrane-bound isoform-like	AX-181922212	38683416	0						*						
	AC17	XP_023860894.1	pro-neuregulin-3, membrane-bound isoform-like	AX-181942722	38714491	0			*									
	AC17	XP_023860894.1	pro-neuregulin-3, membrane-bound isoform-like	AX-181913589	38714498	0						*						
	AC17	XP_023860894.1	pro-neuregulin-3, membrane-bound isoform-like	AX-181974022	38788922	0						*						
	AC17	XP_023860894.1	pro-neuregulin-3, membrane-bound isoform-like	AX-181914524	39021739	0	*											
	AC18*	XP_023864068.1	pro-neuregulin-3, membrane-bound isoform	AX-181914283	21240882	0						*	*					
	AC18*	XP_023864068.1	pro-neuregulin-3, membrane-bound isoform	AX-181942151	21541076	0		*				*	*					*
	AC18*	XP_023864284.1	pro-neuregulin-3, membrane-bound isoform-like	AX-181943495	43996520	0	*											
	AC25*	XP_023825564.1	pro-neuregulin-3, membrane-bound isoform isoform X2	AX-181942348	20692272	0								*			*	
type I isitol 1,4,5-trisphosphate 5-phosphatase	AC18*	XP_023863329.1	type I isitol 1,4,5-trisphosphate 5-phosphatase isoform X2	AX-181926142	29494356	0	*	*			*	*				*		
	AC18*	XP_023863329.1	type I isitol 1,4,5-trisphosphate 5-phosphatase isoform X2	AX-181948291	29497976	0							*		*			
	AC25*	XP_023825797.1	type I isitol 1,4,5-trisphosphate 5-phosphatase-like isoform X2	AX-181939239	7727750	0						*		*				

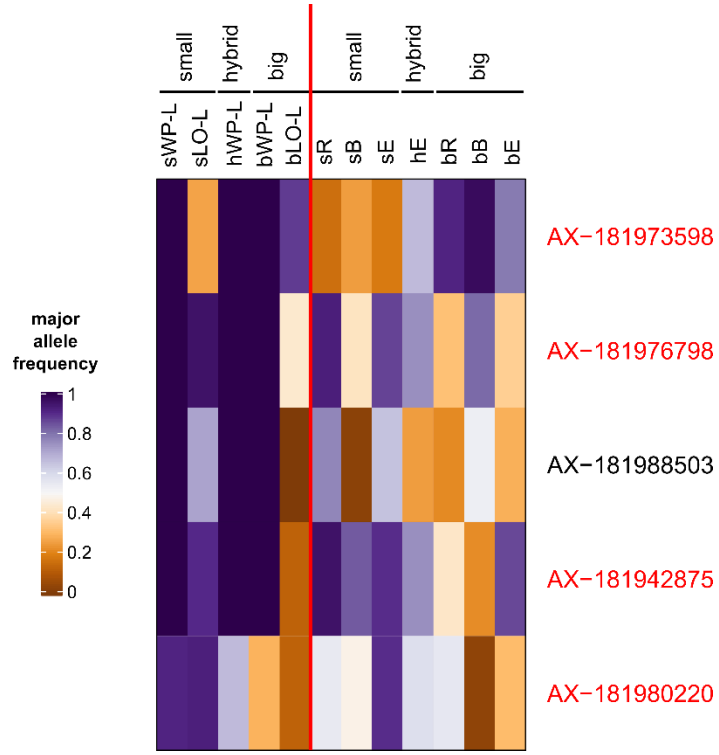


Fig.S5.14 Heatmap of allele frequencies of loci detected as outliers between genetically and size-differentiated sympatric morphs within at least three locations. Morph types (s-small, b-big, h-hybrid) are denoted for each landlocked location (WP-L and LO-L) and locations from Salisbury et al. (2020) (R-Ramah, B-Brooklyn, E-Esker North). The names of SNPs which show parallel allelic trends across the locations in which a SNP was detected as an outlier are highlighted in red.

Table S5.15 Outlier SNPs detected between sympatric small (s) and big (b) morphs in at least three locations of: WP-L, LO-L, Ramah (R), Brooklyn (B), Esker North (E) (latter three populations are from Salisbury et al. (2020)).

						Landlocked		Sea-accessible		
Gene Name	**Linkage Group**	**Protein Code**	**SNP Code**	**Position (bp)**	**Position Relative to CDS (bp)**	**sWP-L vs. bWP-L**	**sLO-L vs. bLO-L**	**sR vs. bR**	**sB vs. bB**	**sE vs. bE**
LOW QUALITY PROTEIN: protein FAM13B-like	AC08	XP_023848065.1	AX-181942875	7470428	0		*	*	*	
neutral and basic amino acid transport protein rBAT	AC08	XP_023849331.1	AX-181988503	46241469	0		*	*	*	
LOW QUALITY PROTEIN: circadian locomoter output cycles protein kaput-like	AC16	XP_023860002.1	AX-181976798	26547496	0		*	*		*
pappalysin-2	AC32	XP_023833607.1	AX-181973598	19625309	0			*	*	*
VPS10 domain-containing receptor SorCS2	AC37	XP_023837960.1	AX-181980220	14860156	0	*	*			*

Table S5.16 Genes for which different paralogous outlier loci were detected between sympatric small (s) and big (b) morphs in at least three locations (one of which must be either WP-L or LO-L) of: WP-L, LO-L, Ramah (R), Brooklyn (B), Esker North (E) (latter three populations are from Salisbury et al. (2020)).

General Gene Name	Linkage Group	Protein Code	Specific Gene Name	SNP Code	Position (bp)	Position Relative to CDS (bp)	sWP-L vs. bWP-L	sLO-L vs. bLO-L	sR vs. bR	sB vs. bB	sE vs. bE
opsin-5-like	AC16	XP_023859543.1	opsin-5-like	AX-181944047	31430031	4687					*
	AC17	XP_023861129.1	opsin-5-like	AX-181972643	5042735	0	*		*		
receptor-type tyrosine-protein phosphatase U	AC30	XP_023990454.1	LOW QUALITY PROTEIN: receptor-type tyrosine-protein phosphatase U	AX-181942714	10297370	0			*		
	NW_019942538.1	XP_023991103.1	receptor-type tyrosine-protein phosphatase U	AX-182168445	456401	0		*			
	NW_019943148.1	XP_023995107.1	receptor-type tyrosine-protein phosphatase U-like	AX-181987996	137217	0					*

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CHAPTER 6 - GEOGRAPHY, ENVIRONMENT, AND COLONIZATION HISTORY INTERACT WITH MORPH TYPE TO SHAPE GENETIC VARIATION IN AN ARCTIC FISH

6.1 Abstract

Species demonstrating a wide range of phenotypic diversity are critical for uncovering the evolutionary mechanisms influencing diversification. Arctic Charr (*Salvelinus alpinus*) is one such species, demonstrating morphological variation in both allopatry and sympatry, including anadromous, resident, and landlocked morphs. Morphs experience different selective pressures, gene flow, and genetic drift due to their different life histories. Historical colonization may have also shaped contemporary genetic structure of Arctic Charr populations as most were colonized only recently, after the last glacial maximum, from five glacial lineages which existed in allopatry during the Pleistocene. Here we used an 87k SNP chip to investigate the population structure and recent historical and contemporary genetic diversities of anadromous, resident, and landlocked charr collected from 45 locations from Labrador as well as Newfoundland and Quebec, Canada. A strong pattern of isolation by distance across all populations suggested geographic distance principally shaped genetic structure across or study area. Within Labrador, landlocked populations had lower genetic diversities and higher genetic differentiation than anadromous populations. However, the genetic diversity in landlocked populations was generally stable through time, while some anadromous populations demonstrated recent decreases in population size suggesting their potential vulnerability to environmental change. Genetic diversity positively correlated with latitude, potentially indicative of the vulnerability of southern anadromous populations to climate change and greater introgression between the Arctic and Atlantic glacial lineages in northern Labrador. Across all populations we uncovered functionally relevant outlier genes associated with temperature, precipitation, diurnal range as well as latitude and elevation suggesting environmentally driven adaptation may also shape genetic differentiation of Arctic Charr. Our results demonstrate that gene flow, colonization history, and local adaptation influence the genetic variation and evolutionary trajectory of each population.

6.2 Introduction

Intraspecific variation in the form of ecologically, phenotypically, and genetically distinguishable morphs offer a unique opportunity to investigate evolution on a contemporary time frame. Since intraspecific variation can be the source of later speciation (West-Eberhard 1986), the diversity within a single species can therefore provide insights into the patterns and processes of diversification across the tree of life. Morphs may demonstrate a difference in ecological effects on communities, sometimes even exceeding that of different species (Bolnick et al. 2011; Des Roches et al. 2018). Morphs may also differ in their economic and cultural value. For example, of the four morphs of Arctic Charr (*Salvelinus alpinus*) in Thingvallavatn, Iceland, the planktivorous morph is preferentially commercially exploited (Snorrason et al. 1992). Understanding the underpinnings of morph differentiation is essential for the preservation of each morph's distinct ecological, economic, and cultural value. Intraspecific morphs have also experienced recent or ongoing gene flow, such that each morph cannot be understood in isolation (Coates et al. 2018). Successful management of species with distinct morphs therefore relies upon an understanding of the genetic and evolutionary relationships among all morphs.

While such radiation events have long inspired biologists, recent advances in genomic techniques have allowed for the uncovering of the genetic causes and consequences of reproductive isolation and adaptive differentiation (Seehausen et al. 2014). Early genetic studies were typically limited to a handful of neutral or adaptive loci but improved genomic resources and sequencing techniques have allowed for the genome-wide assessment of intraspecific variation (Harrisson et al. 2014). These techniques have allowed for greater illumination of the genetic aspects of morph differentiation within a variety of taxa including walking sticks (*Timema spp.*, Nosil 2007; Nosil et al. 2018), Three-spined Stickleback (*Gasterosteus aculeatus*, Marques et al. 2016; Magalhaes et al. 2020), sunflowers (*Helianthus spp.*, Todesco et al. 2020), and periwinkle (*Littorina saxatilis*, Kess et al. 2018, 2020; Galindo et al. 2019).

This work has revealed that multiple processes can influence morph formation and persistence. Ecological speciation, where divergent selection drives reproductive isolation, has been identified as a key contributor to morph differentiation (Schluter

1996a, 1996b). Such adaptive differentiation is particularly likely in those species occupying environments where multiple unoccupied niche spaces are available (such as postglacial environments) and can drive genetic, morphological, and ecological differentiation within species (Smith and Skúlason 1996).

In addition to adaptation, neutral processes such as gene flow and genetic drift can influence morph evolution. For example, dispersal differences between morphs due to selection or environmental happenstance can further drive morph differentiation (Waters et al. 2020). Dispersal may be reduced due to adaptation, such as the evolution of larger seed size to reduce dispersal in island plant populations (Kavanagh and Burns 2014). Alternatively, reductions in dispersal may be entirely neutral, such as one morph being present in more isolated and discontinuous habitats (Waters et al. 2020). For example, migration levels between island populations of Fiji bush-warblers (*Horornis ruficapilla*) could be explained entirely by neutral processes (as a function of island size and distance between islands) rather than selection against migration (Gyllenhaal et al. 2020). Introgression between morphs with differing levels of intra-morph gene flow can still occur in some cases and have important evolutionary consequences. The transporter hypothesis suggests that through hybridization, migratory morphs may be able to move adaptive alleles arising in more isolated morphs across the species range thereby increasing the adaptability of the entire species complex (Schluter and Conte 2009). Genetic diversity may also shape morph divergence. Those morphs with lower genetic diversity differentiate more slowly due to genetic drift. For example, higher genetic diversity and lower genetic differentiation among sea/river-rearing than among lake-rearing Sockeye Salmon (*Oncorhynchus nerka*) may be due to lake environments having lower carrying capacities (though higher gene flow between sea/river-rearing populations may also contribute) (Wood et al. 2008). Different morph types may therefore experience different evolutionary trajectories due to exclusively neutral processes which may either enhance or ameliorate adaptive differences.

Finally, in addition to contemporary processes, historical colonization can also influence morph differentiation. The influence of historical processes is particularly important in recently colonized post-glacial populations, which have not reached an equilibrium state (Svenning and Skov 2007; Vera-Escalona et al. 2015; Ruzzante et al.

2019). During the Pleistocene, some contemporary species were separated into allopatric refugia which have subsequently recolonized post-glacial habitats (Hewitt 2000). The glacial lineages descendant from each refugia may therefore differ genetically resulting in consequences for the evolution of contemporary morphs. For example, wave-adapted periwinkle from two different glacial lineages showed little genetic parallelism, suggesting the independent evolution of this morph in both glacial lineages (Kess et al. 2018). Similarly, sympatric, ecologically-differentiated Arctic Charr (*Salvelinus alpinus*) morphs showed more evidence of parallel genetic differentiation of SNPs between ecotypes within glacial lineages than between glacial lineages (Jacobs et al. 2020). Glacial lineages may come into secondary contact and introgress, resulting in an increase in genetic diversity. For example, expected heterozygosity of the tree *Kalopanax septemlobus* increased from southern to northern Japan but was elevated in northern Honshu, Japan due to secondary contact between two glacial lineages (Sakaguchi et al. 2011). Additionally, in those species recolonizing postglacial habitat, the leading edge of the species may demonstrate reduced genetic diversity due to founder effects (Eckert et al. 2008). The trailing edge of the species may also demonstrate reduced genetic diversity due to reduced gene flow and limited carrying capacities due to environmental constraints (Hewitt 2000; Castric and Bernatchez 2003; Eckert et al. 2008). Therefore, the genetic variation among contemporary morphs may be strongly influenced by colonization history.

One species noted for its intraspecific diversity is Arctic Charr (*Salvelinus alpinus*) which has been called the most variable vertebrate on Earth (Klemetsen 2013). This species has long fascinated and puzzled biologists for its impressive phenotypic variation that has arisen evolutionarily recently, within the last 20000 years (Brunner et al. 2001). The frequent observation of highly phenotypically distinct sympatric charr morphs has even been dubbed the “charr problem” (Nordeng 1983; Klemetsen 2010). Recent work has made great strides in uncovering the genetic and phenotypic differentiation between sympatric morphs within landlocked populations (e.g., Doenz et al. 2019; Jacobs et al. 2020). There has also been significant work on genetic characteristics of anadromous populations (Dallaire et al. 2020; Layton et al. 2020, 2021; Li et al. 2020). The anadromous morph is highly prized in commercial, subsistence, and

recreation fisheries throughout the Arctic (Scott and Crossman 1973; Reist et al. 2006) but is particularly vulnerable to climate change which may favour non-anadromous morphs (Reist et al. 2006; Finstad and Hein 2012; Layton et al. 2021). An additional morph which has been comparatively less-well studied than the anadromous and landlocked morphs is the resident morph. Residents exist in fresh water all year round and they differ from landlocked forms in hat they inhabit environments with access to the sea and occur in sympatry with anadromous morphs (Nordeng 1983; Jonsson and Jonsson 2001). In those populations with sympatric resident and anadromous charr, residency appears to be largely plastic in some locations (Nordeng 1983; Moore et al. 2014) but in other locations these morphs seem to be reproductively isolated (Salisbury et al. 2018; Doenz et al. 2019; O'Malley et al. 2019). Although landlocked, anadromous, and resident morphs can exist in close proximity (Nordeng 1983; Salisbury et al. 2018) the genetic relationship among these different morph types over large spatial scales remains largely uncharacterized (but see Kapralova et al. 2011).

We were therefore interested in investigating the genetic structure of previously identified landlocked, anadromous, and resident morphs across Labrador (Salisbury et al. 2018, 2019, 2020, Chapter 5). The anadromous morph is the basis of an economically and culturally important fishery within Nunatsiavut and subject to Indigenous co-management (Dempson et al. 2008; Snook et al. 2018). There are also multiple locations in Labrador where genetically distinguishable, sympatric morphs are apparent, and typically differentiated by size into a small (s) and big (b) morph, with hybrids (h) sometimes apparent. In some locations these small and big morphs are speculated to be ecologically-differentiated landlocked morphs (Chapter 5) as observed in Quebec (Power et al. 2009). In other sea-accessible locations these small and big morphs may be resident and anadromous morphs, respectively (Salisbury et al. 2020). Historically, Labrador was the site of secondary contact between the Arctic and Atlantic lineages of Arctic Charr (Brunner et al. 2001; Moore et al. 2015; Salisbury et al. 2019). Mitochondrial D-loop haplotypes associated with the Atlantic and Arctic lineages were found within populations across Labrador (Salisbury et al. 2019) suggesting extensive introgression of these glacial lineages in this region despite their divergence between 716000 – 1432000 years ago (Moore et al. 2015). There was also evidence of Acadian glacial lineage

haplotypes in a few southern Labrador populations suggesting limited colonization and introgression by this third glacial lineage (Salisbury et al. 2019). The importance of this secondary contact event on the contemporary genetic structure of charr in the region is unknown. However, different glacial lineages are not associated with particular morph types, as Acadian, Atlantic and Arctic haplotypes were detected in anadromous, resident, and landlocked populations (Salisbury et al. 2018, 2019). Additionally, for all locations with small and big morphs, the character of haplotypes did not differ between sympatric morphs suggesting that they were not founded by different glacial lineages (Salisbury et al. 2018, 2019, 2020, Chapter 5).

Given that Labrador only deglaciated ~ 9000 years BP (Bryson et al. 1969; Occhietti et al. 2011), contemporary Arctic Charr populations have been relatively recently established in this region. The non-anadromous morphs in this region (landlocked, resident), have also evolved from ancestral anadromous populations in this short evolutionary time frame (Power 2002a). While this offers an opportunity to investigate incipient morph differentiation, the likely non-equilibrium state of these populations means that the introgression of multiple glacial lineages in this region may have a lingering influence on contemporary genetic structure of populations and morphs (Bernatchez and Wilson 1998). Neutral processes like gene flow and genetic drift are also likely to differ between morphs, particularly as anadromous individuals are more likely to stray and demonstrate higher gene flow among populations than landlocked or resident morphs (Gyllensten 1985; DeWoody and Avise 2000; Hendry et al. 2004). Finally, the fact that strong environmental gradients are present in Labrador (Barrette et al. 2020; Layton et al. 2021) means that, despite their geographical proximity, Arctic Charr populations in this region may be subject to different environmental selection regimes. We therefore used a newly designed 87k SNP array (Nugent et al. 2019) to investigate the interactive effects of colonization history, neutral processes, and selection on the population genetic structure of Arctic Charr morphs across Labrador, Canada.

6.3 Methods

6.3.1 Sampling

Tissue samples (gill and fin) (N = 1302, Table 6.1) of Arctic Charr were collected between 2010 and 2017 from 45 locations in Newfoundland, Labrador, and Ungava (Fig.6.1). Samples were collected using variable sized standardized nylon monofilament gillnets (1.27–8.89 cm diagonal) or electrofishing. All samples were immediately stored in 95% ethanol or RNAlater.

6.3.2 Extraction, Sequencing, Genotyping and Quality Control

DNA was extracted using either a glassmilk protocol (modified from Elphinstone et al. 2003), a Phenol Chloroform protocol (modified from Sambrook and Russell 2006), or a Qiagen DNeasy 96 Blood and Tissue extraction kit (Qiagen) and quantified using QuantIT PicoGreen (Life Technologies).

DNA samples were sent to the Clinical Genomic Centre of Mount Sinai Hospital (Toronto, Canada) for sequencing using an 87k Affymetrix Axiom Array (Nugent et al. 2019). We employed the "best practices workflow" (according to the Axiom Genotyping Solution Data Analysis Guide) for a diploid organism in Axiom Analysis Suite (Version 4.0.1.9) to analyze the resulting .CEL genomic data files. When using Axiom Analysis Suite to genotype samples we used default sample quality control thresholds: dish quality control ≥ 0.82, quality control call rate ≥ 0.97, and average call rate of passing samples on a given plate ≥ 0.985. We regenerated SNP Metrics using the "Run PS Supplemental" option as recommended (Axiom Analysis Suite User manual version 3.1) for complex genomes to screen out putative paralogous sequence variants given the potential that some regions of the charr genome may remain un-diploidized after the salmonid whole genome duplication. Those SNPs categorized as "PolyHighResolution", "NoMinorHom" and "MonoHighResolution" were used in analyses. Samples from 2010-2015 were extracted in a different lab and sequenced at a separate time from the 2017 samples and were therefore analyzed as separate "batches" in accordance with Axiom Analysis Suite User manual (version 3.1) and the Axiom Genotyping Solution Data Analysis Guide. SNPs with a frequency of one particular allele > 0.95 in one batch but < 0.05 in another were removed in order to exclude those SNPs that were genotyped inconsistently across

the two batches used in this study. Four samples from the 2010-2015 batch were also sequenced and genotyped twice to screen out those SNPs which were not identically genotyped within individuals. Both replicates passed quality control measures in only three of these samples and 321 SNPs were removed from the analysis due to inconsistent scoring among these three pairs of replicate samples. Replicate genotypes of a single individual were combined for those SNPs where one of the two replicates was missing a genotype. After filtering samples, we retained a total of N = 1206 individuals (Table 6.1) for further analyses.

A minor allele frequency (MAF) filter of 0.01 was applied using PLINK (Version 1.9; Chang et al. 2015) across all populations. PGDSpider (Version 2.1.1.5)(Lischer and Excoffier 2012) was used to convert between PLINK and Genepop files and the R package (R Core Team 2013) *genepopedit* (Stanley et al. 2017) was used to order and arrange Genepop files for downstream analyses.

6.3.3 Population Structure Analyses

Earlier work had identified genetic sub-structuring consistent with small (s) and big (b) morphs in five locations in Labrador using the same samples used in this study (Salisbury et al. 2020, Chapter 5). Samples from these locations were therefore designated as small (s), big (b), and (where applicable) hybrid (h) morphs as assigned by Salisbury et al. (2020) or Chapter 5. Genetically homogeneous small and big morphs occurred in each of the neighbouring lakes WP132 and WP133 (locations 14 and 15, respectively in Fig.6.1). Therefore, samples from either lake were grouped together and assigned to either the small, big, or hybrid group (sWP, bWP, hWP, respectively). There was no evidence of genetic differences between samples collected at three locations within the Notakwonan River (W01, W02, W03) (Table S6.1, Fig.S6.1,S6.2), so samples were pooled into a single population W0. All other individuals were assigned to populations based on their sampling location. Samples from our 45 locations were therefore assigned to 49 populations prior to downstream analyses.

Using a common set of SNPs after applying a MAF of 0.01, the genetic structure of all populations was assessed using the R package *PCAdapt* (Version 4.1.0; Luu et al. 2017) testing K = 1-100 with the default Mahalanobis distance. Weighted pairwise F_{ST}s

(Weir and Cockerham 1984) were estimated between all genetic groups using the package *hierfstat* (Goudet 2005) using all filtered SNPs. F_{ST}s were estimated again using putatively neutral loci by excluding outliers using PCAdapt and the RDA analyses described below. The PCAdapt analyses was then redone using an optimal K-value visually identified from the screeplot of the previous analysis and outlier SNPs were then identified based on an $\alpha = 0.05$ after p-values were corrected using the False Discovery Rate (FDR; Storey and Tibshirani 2003) with the R package *qvalue* (Version 2.14.1; Storey 2015). Outliers identified using PCAdapt and from the RDA analyses below were removed before estimating genetic diversity estimates (i.e., heterozygosities and N_e).

To assess and compare the genetic diversity of each genetic group, heterozygosities and historical and contemporary estimates of effective population size (N_e) were estimated. For each genetic group, observed and expected heterozygosities (H_O, H_E) were estimated for each SNP using PLINK and then averaged. To investigate historical changes in genetic diversity we used LinkNe (Hollenbeck et al. 2016) a method which uses linkage disequilibrium to estimate historical N_e as a function of recombination rate. We ran LinkNe using a common set of SNPs that passed the initial global MAF of 0.01 and had a known recombination rate based on an uncharacterized *Salvelinus sp.* genome (Christensen et al. 2018; NCBI assembly ASM291031v2). We used the default MAF cut-off of 0.05 (applied independently to each population) and the default bin size of 0.05 Morgans. Any negative 95% parametric confidence interval estimates and $\widehat{N}_{e(\text{LinkNe})}$ resulting from the LinkNe analyses were designated as "infinite". The same set of SNPs used for the LinkNe analyses were also used to estimate $\widehat{N}_{e(\text{NeEstimator})}$ using the linkage disequilibrium method with NeEstimator v2.1 (Do et al. 2014) (again, using a MAF cut-off of 0.05 for each population), and 95% confidence intervals were calculated using the jackknife method.

To investigate for the effects of geographic distance on genetic structure, and particularly to look for evidence of isolation by distance (IBD), we performed a Mantel test. We generated a pairwise geographic distance matrix between all genetic groups using the "distm" function of the *geosphere* R package (Hijmans et al. 2017) based on latitude and longitude of each sampling location. Some genetic groups which occurred in sympatry with other groups (i.e., those locations with small and big morphs) therefore

had geographic distances of zero. The latitude and longitude of the genetic groups which included samples from multiple locations (i.e., W0, sWP, bWP, hWP) were averaged over the locations where samples contributing to each genetic group was collected. We recognize that pairwise distances calculated based on latitude and longitude may underestimate the true distance experienced by a fish between locations. However, this approach is justified given the large distances between most locations (>100 km) and the potential for the hydrology between sites to have changed significantly during deglaciation of this region ~9000 years ago (Bryson et al. 1969; Occhietti et al. 2011). A Mantel test to assess for a significant correlation between pairwise F_{ST}s and pairwise geographic distances was conducted using the R package *cultevo* (Stadler 2018) using the default Spearman method and 9999 trials.

To further investigate the effects of geographic distance as well as those of environmental variables on genetic structure we conducted a Redundancy Analysis (RDA). We downloaded data for the 19 "bioclimatic" variables and elevation from the WorldClim v2.1 database (Fick and Hijmans 2017). We used a resolution of 30 seconds for all locations except two (HAB, R78) for which we used a resolution of 2.5 minutes as no data was available at 30 seconds resolution. For those genetic groups which were collected in multiple locations (W0, sWP, bWP, hWP) climatic and elevation data were averaged across sampling locations. We assessed for correlation among elevation and climatic variables, removing climatic variables until no variables had a correlation (as measured using the Pearson correlation coefficient) > 0.75 with any other variable. Missing genotypes were imputed as the most common genotype for each SNP. We then conducted an RDA using the R package *vegan* (Oksanen et al. 2013) to assess the genetic variation explained by latitude, longitude, elevation, and each of the remaining climatic variables. We assessed the significance of the entire RDA correlation as well as for each of the variables using the anova.cca() function of the *vegan* package, using 999 permutations for each analysis. We investigated for putative outlier SNPs identified as those that loaded > 3 SD from the mean distribution of each of those RDAs explaining the majority of the genetic variation. We identified the closest gene < 5000 bp from each of these outlier SNPs based on a genome for an uncharacterized *Salvelinus sp.* (Christensen et al. 2018; NCBI assembly ASM291031v2).

6.4 Results

The number of SNPs that passed filtering after applying a MAF of 0.01 was N = 22935. The first two PCs from our PCAdapt analysis explained a combined 11% of the data and roughly separated all populations consistent with their geographic locations (Fig.6.2). Specifically, the latitudinal position of populations increases from the lower left to the upper right quadrat of the PCA. The anadromous Ungava population (HAB) and three anadromous southern populations (PBP, MBB, ENG) are located at opposite corners of the PCA indicating their genetic distinctiveness. Within the northern Labrador, individuals from anadromous populations form a conspicuous "smear" where populations are ordered by latitude between the Southern and Ungava populations. Orthogonal to this roughly continuous line of anadromous populations are a series of isolated, genetically distinguishable populations. Most of these populations are known to be landlocked (based on Anderson 1985). However, several populations with apparent sea-access (based on Anderson 1985) are also included in this group including H16, small morphs within Ramah (sR) and all morphs within Esker North (sE, bE, hE) and Brooklyn (sB, bB). The life history of these populations with respect to anadromy is uncertain, however, given their genetic distinctiveness from known anadromous populations, these populations may comprise non-anadromous individuals. As previously noted in Chapter 5 the genetic similarity of the big morphs from Ramah (bR) but not those from Esker North (bE) and Brooklyn (bB) with nearby anadromous populations suggests that the big morphs from the latter two populations may not be currently anadromous as had been suggested by Salisbury et al. (2020). We therefore refer to this group of populations as the "Resident/Landlocked" PCA group henceforth, with the acknowledgement that the life history of some populations is uncertain. The PCA therefore suggests four groups of populations: Ungava (U), Northern Labrador Anadromous (A), Northern Labrador Resident/Landlocked (R), Southern (S). Pairwise F_{ST}s were nearly identical using all SNPs (N = 22935 SNPs) and excluding putative outliers detected using PCAdapt and RDA (N = 22259 SNPs, see below for more details), therefore only results using all SNPs are reported (but see Supporting Information for results using putative neutral SNPs only Fig.S6.3-S6.5). Weighted pairwise F_{ST}s were notably higher between populations within

the U, S, and R PCA groups relative to those of A populations, supporting the genetic isolation of populations within the first three groups (Fig.6.3).

Based on the screeplot for the initial PCA using K = 100 PCs (Fig.S6.6), a reduced K-value of 6 was chosen for outlier selection. A total of 560 outlier SNPs were detected from the PCAdapt analysis, a further 144 SNPs were identified from the RDA (see below) with 30 SNPs detected by both outlier detection methods. These 676 unique outlier SNPs detected across both methods were removed before estimating heterozygosity and N_e values.

H_E and H_O ranged from a low of 0.05 for both estimates in the most southern anadromous population PBP, to a high of 0.30 for both estimates in the anadromous population MCC (Fig.6.4a). $\widehat{N}_{e(\text{NeEstimator})}$ ranged from a low of 24.2 in the anadromous population KIY to a high of 617.8 in the putative resident sR population (Fig.6.4b) (for all results see Table S6.2).

Results of all LinkNe analyses based on up to 1105 polymorphic SNPs are shown in Fig.S6.7, Table S6.2. Infinite $\widehat{N}_{e(\text{LinkNe})}$ and/or 95% confidence intervals for some populations may be due to relatively small sample sizes (e.g., hWP (N = 6), bLO (N = 8), hE (N = 6), GB (N = 10), SLU (N = 12), W0 (N = 21)). Alternatively, several populations (KAN, MCC, sR, PAN, R104, IKL, MBB) demonstrated infinite $\widehat{N}_{e(\text{LinkNe})}$ and/or 95% parametric confidence intervals within the last four generations, which might indicate a rapid increase in population size or a recent introgression event. For clarity, only those populations with non-infinite $\widehat{N}_{e(\text{LinkNe})}$ and 95% parametric confidence intervals for all four time points (1.5, 4, 6.7, 20 generations in the past) are shown in Fig.6.5. Of those populations with non-infinite $\widehat{N}_{e(\text{LinkNe})}$ and 95% parametric confidence intervals for all four time points more populations within the A PCA Group demonstrated an increase in $\widehat{N}_{e(\text{LinkNe})}$ between 4 to 1.5 generations ago than those within the R Group (6/11 vs. 20/22, respectively). Although no populations had an $\widehat{N}_{e(\text{LinkNe})} > 500$ 4 generations ago, 6/22 populations from the A PCA Group but no populations from the R PCA Group had an $\widehat{N}_{e(\text{LinkNe})} > 500$ 1.5 generations ago. The $\widehat{N}_{e(\text{LinkNe})}$ of the Ungava population (HAB) declined slightly from 20 generations ago to 1.5 generations ago, whereas in the S PCA Group, one population's $\widehat{N}_{e(\text{LinkNe})}$ (ENG) declined while the other (PBP) remained relatively constant from 20 to 1.5 generations ago.

While both H_E and H_O were significantly correlated with latitude in populations within the A PCA Group ($t_{26} = 10.823$, $t_{26} = 11.698$, and $p < 0.01$, $p < 0.01$, respectively), they were not significantly correlated with latitude in populations within the R PCA Group ($t_{15} = -0.003$, $t_{15} = -0.073$, and $p > 0.99$, $p = 0.94$, respectively) (Fig.6.6a,b). Both H_E and H_O were significantly higher in populations within the A PCA Group than within the R PCA Group, after adjusting for latitude ($F_{1,42} = 80.038$, $F_{1,42} = 83.232$, and $p < 0.01$, $p < 0.01$, respectively). The Ungava population (HAB) had a notably lower H_E and H_O than those populations within the A Group at similar latitudes. H_E and H_O increased with latitude in the three anadromous populations within the S PCA Group which generally had lower H_E and H_O than those populations in the A PCA Group. Similar trends were also observed for $\widehat{N}_{e(\text{NeEstimator})}$ after removing populations with infinite upper 95% jackknife confidence intervals as well as a high and potential outlier $\widehat{N}_{e(\text{NeEstimator})}$ for the sR population (Fig.6.6c, for all populations see Fig.S6.8). $\widehat{N}_{e(\text{NeEstimator})}$s were significantly higher in populations within the A PCA Group than within the R PCA Group, after adjusting for latitude ($F_{1,33} = 8.044$, $p < 0.05$). $\widehat{N}_{e(\text{NeEstimator})}$ positively, but not significantly, correlated with latitude in populations within the A PCA Group ($t_{25} = 1.20$, $p = 0.24$). This correlation was also not significant within R PCA Group ($t_7 = -1.3$, $p = 0.24$). The Ungava population (HAB) had a notably lower $\widehat{N}_{e(\text{NeEstimator})}$ than those populations within the A PCA Group at similar latitudes. $\widehat{N}_{e(\text{NeEstimator})}$ increased with latitude in the two anadromous populations within the S PCA Group which generally had lower $\widehat{N}_{e(\text{NeEstimator})}$ than those populations in the A PCA Group.

A significant correlation was detected between pairwise F_{ST} and pairwise geographic distances using a Mantel test for all populations ($r = 0.288$, $p < 0.01$) (Fig.6.7a) but not when including only populations from the A and R PCA Groups ($r = 0.087$, $p = 0.14$) (Fig.6.7b, see Fig.S6.9 for comparisons between all PCA groups). However, when R vs. R, R vs. A, and A vs. A pairwise comparisons were considered separately, all three groups demonstrated a significant linear regression between pairwise F_{ST} and pairwise geographic distance ($t_{134} = 5.118$, $p < 0.001$; $t_{474} = 2.113$, $p < 0.05$; $t_{376} = 20.62$, $p < 0.001$). In addition, the y-intercept of the regression line was greatest in R vs. R comparisons (0.24), intermediate in R vs. A comparisons, and lowest in A vs. A comparisons (0.03) while the slope of the regression line was greatest in R vs. R

comparisons (0.0009), intermediate in A vs. A comparisons (0.0002), and lowest in R vs. A comparisons (0.0001).

After assessing the correlation between all World Clim variables (Fig.S6.10), we retained the following explanatory variables in our final RDA (Fig.6.8): latitude, longitude, elevation, BIO1 (Annual Mean Temperature), BIO2 (Mean Diurnal Range), BIO7 (Temperature Annual Range), BIO8 (Mean Temperature of Wettest Quarter), BIO9 (Mean Temperature of Driest Quarter), BIO12 (Annual Precipitation). No correlation between any of the selected climatic (BIO) variables > 0.75. The RDA model significantly explained the genetic variation ($F_{9,1196} = 20.154$, $p < 0.01$) and the first two RDA components explained a combined 63.46% of the genetic variation (Fig.S6.11). All explanatory variables significantly explained the genetic variation (all $p < 0.01$, Table S6.3). However, the 144 outlier SNPs associated with either RDA1 or RDA2 were found to be most strongly associated with only latitude (42 SNPs), BIO1 (13 SNPs), BIO2 (2 SNPs), BIO12 (26 SNPs), and elevation (61 SNPs) (Table S6.4).

6.5 Discussion

Our results demonstrate that the genetic structure of Arctic Charr populations is broadly shaped by geography and tempered by each populations' apparent migratory life history. Colonization history and local adaptation have also each influenced the genetic variation across this species' range. The interaction of these forces has resulted in unique evolutionary trajectories for different populations of Arctic Charr.

6.5.1 Genetic Variation Across and Within Sampling Regions

The importance of geography in shaping genetic structure regardless of migration strategy is evident from the clear latitudinal cline in genetic variation in the PCA and the strong signal of IBD across all populations. Similar range-wide patterns of IBD have been commonly reported for other anadromous fishes (Hendry et al. 2004; Bradbury and Bentzen 2007).

Within the northern Labrador populations, there were clear differences in genetic variation between the Anadromous and Resident/Landlocked PCA Groups. Anadromous populations had lower pairwise F_{ST}s, clustered more closely together within the PCA, and

generally had higher H_E, H_O, and $\widehat{N}_e$. IBD among anadromous populations was supported by a significant regression between geographic distance and F_{ST}s. However, the rate of increase in F_{ST} with geographic distance was lower between anadromous populations (A vs. A comparisons) than between resident/landlocked populations (R vs. R comparisons) suggesting higher gene flow among the former. These results confirm the low levels of genetic differentiation previously observed between anadromous Arctic Charr populations (Bernatchez et al. 1998; Moore et al. 2013, 2017). These results are consistent with the potential for straying among anadromous fishes (Hendry et al. 2004) and the inherent isolation and propensity for genetic drift in freshwater populations (Gyllensten 1985; DeWoody and Avise 2000). Landlocked populations demonstrate lower genetic diversity and higher genetic distinctiveness than their allopatric anadromous counterparts in Atlantic Salmon (*Salmo salar*, Tonteri et al. (2007)) and Alewife (*Alosa pseudoharengus*, Palkovacs et al. (2008)). Similarly, resident freshwater populations in *Galaxias maculatus* (Delgado et al. 2019, 2020), Three-Spined Sticklebacks (Drevecky et al. 2013), and Atlantic Salmon (Perrier et al. 2013) are also known to maintain reproductive isolation from anadromous populations, even when they occur in sympatry.

The significant correlation between pairwise F_{ST}s and geographic distance detected among resident/landlocked populations (R vs R comparisons) may reflect the recent colonization of these populations (within the last 9000 years since deglaciation of Labrador (Bryson et al. 1969; Occhietti et al. 2011)), such that they are in a non-equilibrium state (Slatkin 1993; Bernatchez and Wilson 1998) and drift has yet to erode this signature of IBD. The significant correlation in geographic and genetic distances between R vs. A comparisons might similarly be explained by the resident/landlocked populations being recently founded by geographically proximate anadromous populations. Alternatively, northern Labrador has been previously identified as a region of secondary contact and introgression between the highly genetically divergent Arctic and Atlantic glacial lineages (which diverged between 716000 – 1432000 years ago, Moore et al. (2015)). While the mtDNA haplotypes of both glacial lineages are pervasive throughout northern Labrador (Salisbury et al. 2019), this may not reflect introgression of nDNA. We speculate that the point of greatest introgression between the Arctic and

Atlantic lineages might have occurred in northern Labrador, with reduced introgression of Arctic lineage nDNA with decreasing latitude along the Labrador coast. Therefore, the signature of IBD we detect for landlocked populations could reflect more Arctic nDNA in northern landlocked populations than southern landlocked populations.

6.5.2 Genetic Variation Among Anadromous Populations by Region

H_E, H_O, and $\widehat{N}_e$ were lower within the three southern populations (with the exception of the very high $\widehat{N}_{e(\text{NeEstimator})}$ observed in MBB) than in northern Labrador anadromous populations. Selection against anadromy in these southern populations (Finstad and Hein 2012; Layton et al. 2021) could have resulted in reduced genetic diversity due to selective sweeps or reduced gene flow. Similarly reduced genetic diversity in southern anadromous populations of Brook Trout (*Salvelinus fontinalis*) have been attributed to reduced straying relative to northern populations (Castric and Bernatchez 2003). Alternatively, these populations are south of the known limit of the Arctic glacial lineage introgression (Salisbury et al. 2019) and the lower genetic variation observed in these populations may be due to the Arctic lineage not colonizing these populations.

Colonization history might also explain the correlation in heterozygosity, and to a lesser extent $\widehat{N}_{e(\text{NeEstimator})}$, with latitude observed in the anadromous charr populations from northern Labrador. If the point of secondary contact of the Arctic and Atlantic glacial lineages occurred near the northernmost Labrador populations sampled here, this might explain the observed correlation of latitude with diversity, particularly if nuclear genetic variation from the Arctic lineage failed to introgress very far into southern Labrador. We cannot rule out that this cline in diversity was driven by reduced carrying capacity, selective sweeps, or reduced gene flow in more southern populations or recent increases in $\widehat{N}_e$ in more northern anadromous populations (Fig.S6.7). However, the Ungava population (HAB) demonstrated reduced estimates of H_E, H_O, and $\widehat{N}_e$ relative to Northern Labrador populations at similar latitudes suggesting that the increased diversity in northern Labrador populations is not only a function of greater carrying capacities at higher latitudes. In addition, unlike the northern Labrador populations, the Ungava population is presumed to have been founded only by the Arctic lineage (Dallaire et al.

2020), which has less genetic diversity than the other charr glacial lineages (Moore et al. 2015). In addition, a decline in heterozygosity with distance from Labrador was also observed in Nunavik and Baffin Island Arctic Charr populations (Dallaire et al. 2020). This suggests that northern Labrador may be the point of secondary contact between the Arctic and Atlantic lineages, though more geographically extensive sampling beyond this secondary contact zone is needed to further test this hypothesis. Although this cline in diversity with latitude was not also observed in populations within the Resident/Landlocked PCA Group, this signature of colonization may have been erased in these isolated populations due to drift. Therefore, the genetic variation of anadromous Arctic Charr populations across our sampling region may be influenced by colonization history in addition to contemporary reductions in gene flow due to geographic distance.

6.5.3 Historical Changes in $\widehat{N}_e$

LinkNe results revealed varying patterns of $\widehat{N}_{e(\text{LinkNe})}$ change in the last 20 generations across populations. Because generation times may differ between migratory and non-migratory charr (Tallman et al. 1996) and by latitude (Venne and Magnan 1989) it is difficult to directly compare $\widehat{N}_{e(\text{LinkNe})}$ results across populations. However, overall, our results suggest a recent, rapid increase in $\widehat{N}_{e(\text{LinkNe})}$ in many anadromous populations as previously observed by Layton et al. (2021) (who used the same samples from the anadromous populations sampled in 2017 that were also used in this study). However, $\widehat{N}_{e(\text{LinkNe})}$s seem to have remained more stable through time for populations in the Resident/Landlocked PCA Group. However, a sharp increase in $\widehat{N}_{e(\text{LinkNe})}$ was observed in the putative resident morph in Ramah (sR) which also had an unusually high $\widehat{N}_{e(\text{LinkNe})}$. This might be due to a recent increase in population size or recent introgression with the putative anadromous morph in Ramah (bR) (although no hybrids were identified in our samples). Resident morphs occurring in sympatry with anadromous morphs may therefore demonstrate higher genetic diversity than landlocked populations due to occasional introgression with sympatric anadromous morphs. Alternatively, recent reductions in $\widehat{N}_{e(\text{LinkNe})}$ and low $\widehat{N}_{e(\text{NeEstimator})}$ for anadromous KIY, ENG, and ANA populations suggest that these pops may be vulnerable to extinction. This is particularly

concerning for ANA which is a commercially harvested population given its proximity to the main Arctic Charr fishery based out of Nain (Dempson et al. 2008).

6.5.4 Environmentally Associated Adaptation

Our results also support the potential importance of local adaptation in driving genetic variation across Arctic Charr populations. The RDA results suggest that the environmental variables annual temperature (BIO1), annual precipitation (BIO12), and to a lesser extent Mean Diurnal Range (BIO2), were associated with putative outlier loci. The importance of temperature and precipitation in shaping genetic structure of this species is not unexpected given Arctic Charr is a cold-adapted species with lower upper thermal tolerances than other salmonids (Elliott and Elliott 2010) and increased precipitation may drive increased terrestrial primary productivity which has been suggested to be a key driver of residency (Finstad and Hein 2012). Elevation was also associated with outlier loci and was the environmental variable most strongly associated with the genetic differences between the Anadromous and Resident/Landlocked PCA Groups within northern Labrador. This is consistent with populations at higher elevations being more likely to be landlocked or to experience increased migratory energy costs thereby favoring residency (Hendry et al. 2004).

Of the 144 outlier SNPs detected by the RDA, 14 were also previously identified in Chapter 5 as outliers between at least 5/7 pairwise comparisons between landlocked and anadromous charr populations within the same drainage (all of which were also included in this study's analysis). Of these SNPs, 11 were most strongly correlated with elevation in our RDA. This included 4 genes on AC21 including myomesin-2 (associated with cardiac and fast-twitch muscle function (Schoenauer et al. 2008)), lengsin (associated with vertebrate eye lens development (Wyatt et al. 2006)), calpain-9, and uncharacterized protein LOC111982472.

Five of the RDA outlier SNPs also found to be repeatedly differentiated between landlocked and anadromous charr populations in Chapter 5 were detected on AC17. One such SNP associated with elevation fell within the gene inactive dipeptidyl peptidase 10. This gene regulates potassium in neurons (Jerng et al. 2004) and genetically differentiates resident and diadromous populations of *Galaxias maculatus* in Chile (Delgado et al.

2019, 2020). This SNP was also detected as an outlier in Ramah lake between small, putative resident morphs (sR) and big, putative anadromous morphs (bR). The other four such SNPs on AC17 were most strongly associated with elevation (AX-181916309) or annual temperature (BIO1) (AX-181916308, AX-181980622, AX-181983398). Two of these SNPs (AX-181980622, AX-181983398) were also detected as outliers in Ramah lake between sR and bR morphs near the gene. A third SNP (AX-181916308) was detected as an outlier in Esker North lake between small (sE) and big (bE) morphs. The sympatric morphs within Esker North and Ramah could not have driven these SNPs to be detected as outliers in the RDA since sympatric morphs were assigned the same location and associated environmental variables. It is therefore intriguing that these five SNPs which seems to be associated with temperature and elevation differences across a wide geographical range of charr populations may also play a role in the genetic divergence of sympatric morphs. In addition, these outlier SNPs lie within a region of AC17 (~300 kb) previously noted to consistently genetically differentiate paired landlocked and anadromous populations of Arctic Charr in Labrador and putative resident and anadromous charr in Ramah lake (Chapter 5). This region therefore warrants further investigation as it may play a key role in temperature adaptation and migratory life history.

6.5.5 Conclusion

Arctic Charr populations across the studied range are driven by the interactive effects of contemporary gene flow, historical colonization, and local adaptation. Geographical distance is the primary driver of genetic differentiation across the studied area, but within Labrador, the loss of anadromy in some populations has significantly altered their evolutionary trajectories in comparison to anadromous populations (Chapter 5, Delgado and Ruzzante 2020). The widespread historical introgression of the Arctic and Atlantic glacial lineages within Labrador have potentially contributed to the elevated genetic diversity observed within contemporary anadromous populations in this region relative to those in more southern populations and Ungava. As a result, Labrador populations may be less vulnerable to future environmental changes. Our results, along with those of others (Vera-Escalona et al. 2015; Salisbury et al. 2016; Ruzzante et al.

2019), therefore indicate the key role colonization history can play in determining post-glacial population's genetic structure and capacity to respond to environmental changes. This work also highlights the utility of considering multiple morph types across a species range which can give a more informed picture of the genetic structure of a species. Although northern Labrador populations within the Resident/Landlocked PCA Group seem to be subject to greater genetic drift, $\widehat{N}_e$ seem stable through time, although they are lower on average than in anadromous populations. Yet the high $\widehat{N}_e$ of resident morphs in Ramah bodes well for the continued persistence of the resident populations. In addition, increased temperatures and primary productivity are likely to increasingly select against anadromy (Reist et al. 2006; Finstad and Hein 2012), though non-migratory morphs are still temperature sensitive and vulnerable to future climate change (Kelly et al. 2020). Alternatively, while many Labrador anadromous populations have seen a recent surge in $\widehat{N}_{e(\text{LinkNe})}$, some have shown concerning declines. Anadromous populations may be more vulnerable than non-migratory populations since they are exposed to selective pressures in both freshwater and saltwater environments (Limburg and Waldman 2009). Evidence for genetic parallelism between sympatric morphs and allopatric landlocked and anadromous populations (Salisbury et al. 2020, Chapter 5) as well as the range-wide environmentally-associated outlier SNPs detected in this study indicate adaptive differentiation between morphs and across populations. Further investigation of the developmental consequences of these outliers will be critical to the management of all morph types in the face of climate change.

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6.7 Tables

Table 6.1 Sample location information. Note that some sampling locations contain multiple genetic groups and some genetic groups occurred in multiple sampling locations. Sampling location access was either sea-accessible (A) or landlocked (L) as characterized by Anderson (1985) for all Labrador samples. PCA Group assigned to each genetic group include: Ungava (U), Northern Labrador Anadromous (A), Northern Labrador Resident/Landlocked (R), Southern Labrador and Newfoundland (S) (see results for further details).

Site	Name	Latitude (°N)	Longitude (°W)	Year	Access	N	Number of genetic groups	Genetic Group Code	PCA Group	N Passing QC
1	Hope Advance Bay	59.30191	-69.609050	2017	A	30	1	HAB	U	29
2	Kangalaksiorvik River	59.38715	-64.2668	2017	A	30	1	KAN	A	30
3	Komaktorvik	59.22694	-64.0092	2017	A	30	1	KOM	A	28
4	Kogarsok River	59.10934	-63.911	2017	A	30	1	KOG	A	30
5	Nachvak River	58.97935	-64.2381	2017	A	30	1	NAC	A	30
6	McCormick's River	58.97814	-63.6984	2017	A	30	1	MCC	A	30
7	Palmer River	58.92509	-63.8775	2017	A	30	1	PAL	A	30
8	Stecker River	58.86846	-63.4575	2017	A	30	1	STC	A	30
9	Ramah Lake	58.84138	-63.4774	2014	A	61	2	sR	R	32
								bR	A	28
10	North Arm River	58.57114	-63.4974	2017	A	30	1	NOR	A	30
11	Southwest Arm	58.46825	-63.6462	2017	A	30	1	SWA	A	30
12	Kiyuktok River	58.39627	-62.9823	2017	A	30	1	KIY	A	28
13	Pangertok River	58.32611	-63.2087	2017	A	30	1	PAN	A	30
14	WP132 Lake	58.28016	-63.9693	2014	L	30		sWP	R	28
15	WP133 Lake	58.27167	-64.0314	2014	L	28	3	bWP	R	24
								hWP	R	6
16	River 109	58.22318	-63.6706	2017	A	30	1	R109	A	30
17	Ikarut River	58.16057	-63.1614	2017	A	30	1	IKA	A	25
18	Hebron Lake	58.14611	-63.5913	2015	L	30	1	HEB	R	30
19	River 105	58.06341	-63.6845	2017	A	30	1	R105	A	30
20	River 103	58.03142	-63.0371	2017	A	30	1	R103	A	29
21	River 104	57.95381	-63.56	2017	A	30	1	R104	A	29
22	Todayfivk Lake	57.74385	-63.353	2015	A	21	1	H16	R	18
23	Brooklyn Lake	57.72648	-62.4734	2015	A	60	2	sB	R	42
								bB	R	16
24	Beachy Strip Lake	57.66161	-62.9544	2015	L	30	1	BS	R	29
25	Lonely Lake	57.63915	-63.2329	2015	L	30	2	sLO	R	21
								bLO	R	8
26	North River	57.50159	-62.7432	2015	A	30	1	K05	A	29
27	Ikinet River	57.40427	-62.6411	2017	A	30	1	IKI	A	27
28	Puttuaalu River	57.25526	-62.2207	2017	A	30	1	PUT	A	24

Table 6.1 Continued.

Site	Name	Latitude (°N)	Longitude (°W)	Year	Access	N	Number of genetic groups	Genetic Group Code	PCA Group	N Passing QC
29	Esker North Lake	57.14884	-62.8782	2015	A	60	3	sE	R	33
								bE	R	21
								hE	R	6
30	Kingurutik River	56.84256	-62.6216	2017	A	30	1	KIN	A	24
31	Kamanatsuk River	56.75377	-62.5381	2017	A	30	1	KAM	A	29
32	Fraser River	56.69082	-63.465	2017	A	30	1	FRA	A	23
33	Knumandi Lake	56.58141	-63.3234	2011	L	20	1	KNU	R	16
34	Anaktalik River	56.49753	-62.9331	2017	A	30	1	ANA	A	30
35	Slushy Lake	56.41561	-64.1022	2010, 2011, 2012, 2013	L	11	1	SLU	R	10
36	Ikadlavik River	56.3126	-62.1688	2017	A	30	1	IKL	A	17
37	Reid River	56.30319	-62.0852	2017	A	30	1	REI	A	9
38	Genetics B Lake	56.11067	-63.3886	2010, 2011	L	13	1	GB	R	12
39	Notakwonan River Site a	55.97279	-61.7544	2015	A	3				
40	Notakwonan River Site b	55.9334	-62.0709	2015	A	12	1	W0	A	21
41	Notakwonan River Site c	55.90273	-62.1129	2015	A	8				
42	River 78	55.64627	-60.6898	2017	A	30	1	R78	A	24
43	English River	54.96969	-59.7494	2017	A	30	1	ENG	S	30
44	Muddy Bay Brook	53.62977	-57.0299	2017	A	30	1	MBB	S	26
45	Parkers Pistolet	51.49828	-55.7327	2017	A	15	1	PBP	S	15

6.8 Figures

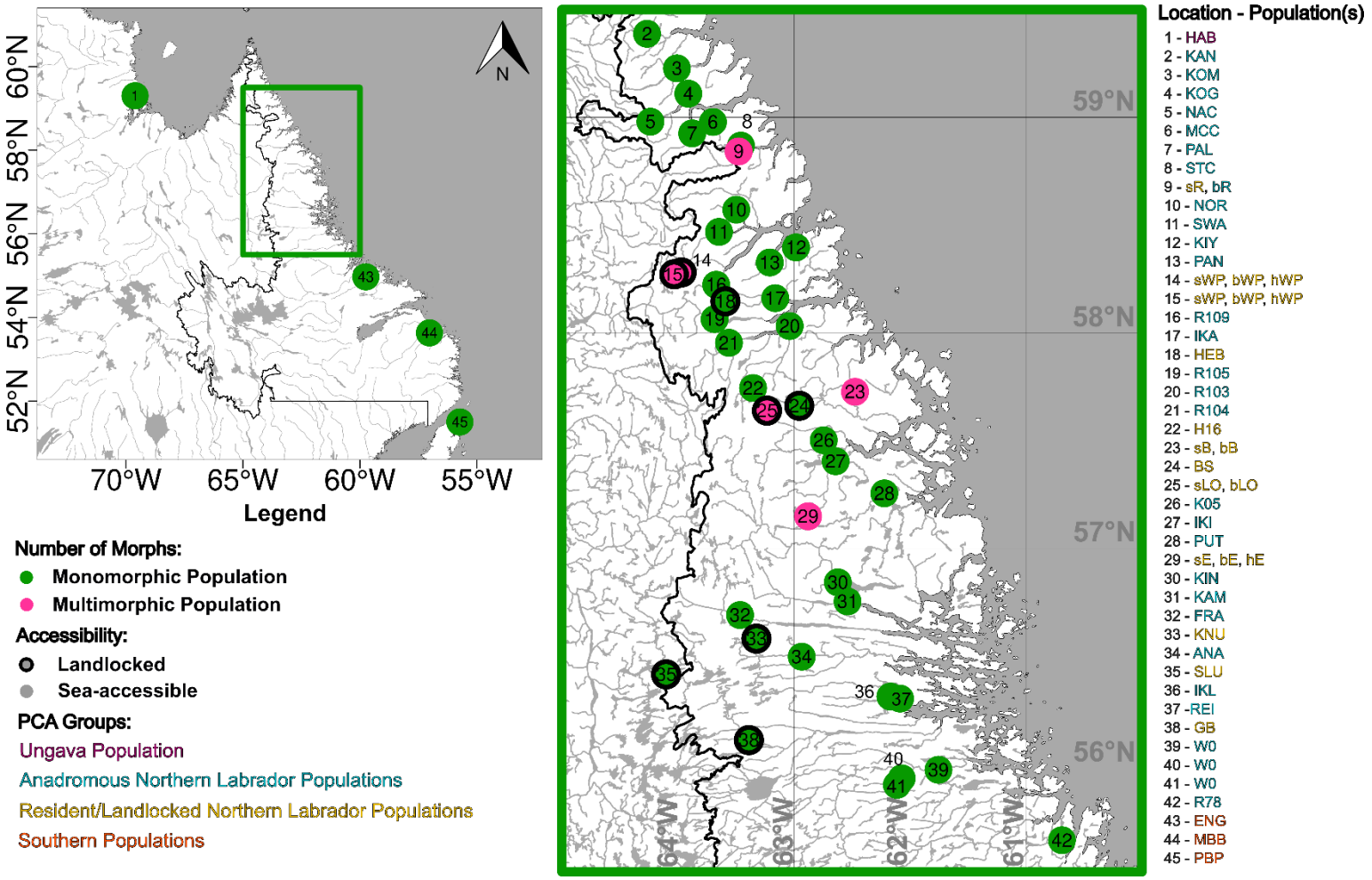

Fig.6.1 Map of 45 sampling locations. The 49 Arctic Charr populations found within each of the sampling location are labeled and coloured by their assigned PCA Group. Map generated using data from CanVec (Government of Canada).

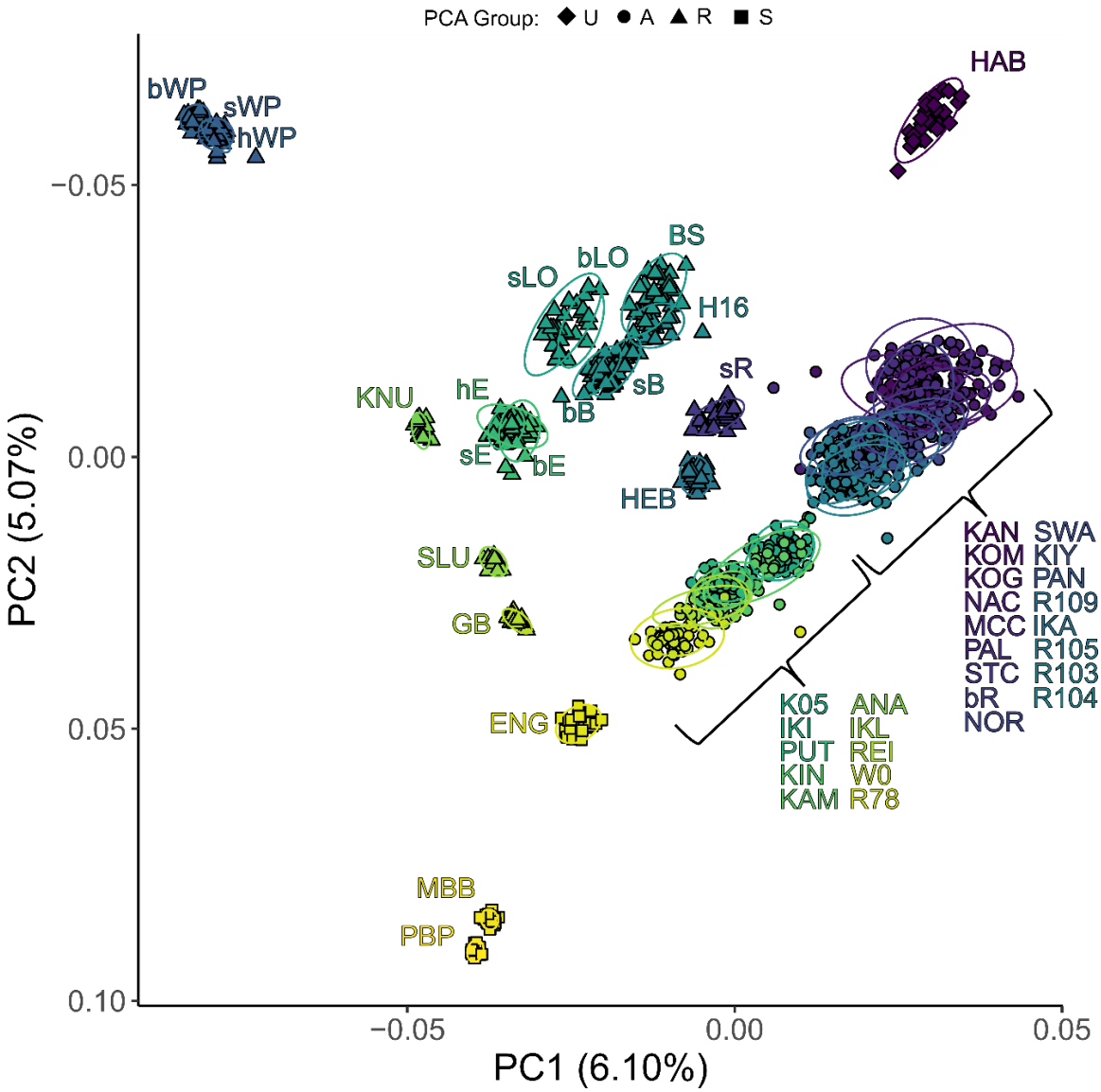

Fig.6.2 PC1 vs. PC2 of genetic variation in 1206 samples within 49 Arctic Charr populations (N = 22935 SNPs) based on PCAdapt analysis of 100 PCs. Shape of points indicate the assigned PCA genetic group: Ungava (U), Northern Labrador Anadromous (A), Northern Labrador Resident/Landlocked (R), Southern Labrador and Newfoundland (S). Circles indicate 95% normal ellipses for each population. Populations are coloured from purple to yellow starting with the Ungava population (HAB) and then from north to south.

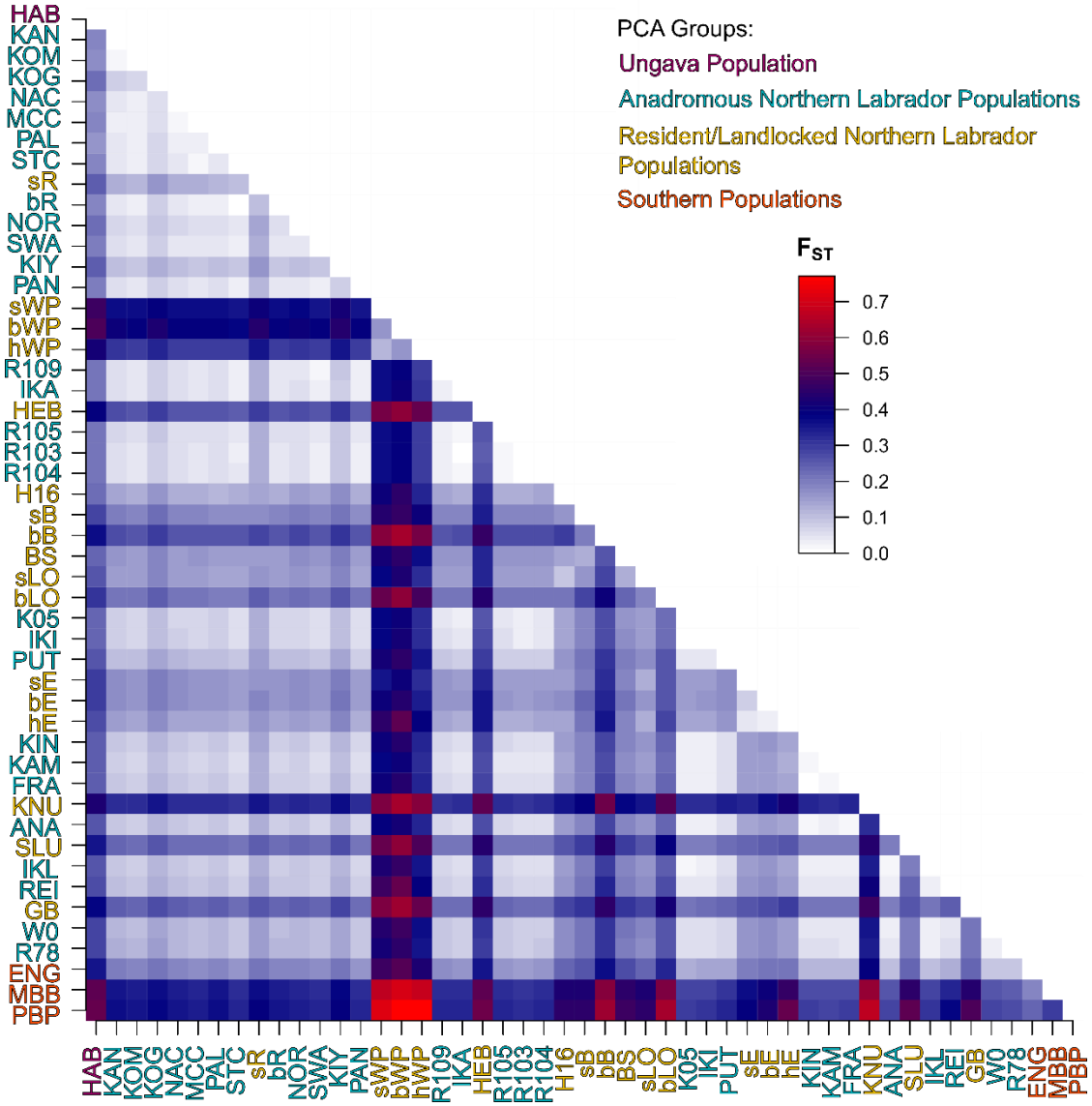

Fig.6.3 Pairwise weighted Weir and Cockerham (1984) F_{ST}s between 49 populations of Arctic Charr using 22935 SNPs. Population labels are coloured based on assigned PCA Group and ordered starting with the Ungava population (HAB) and then from north to south.

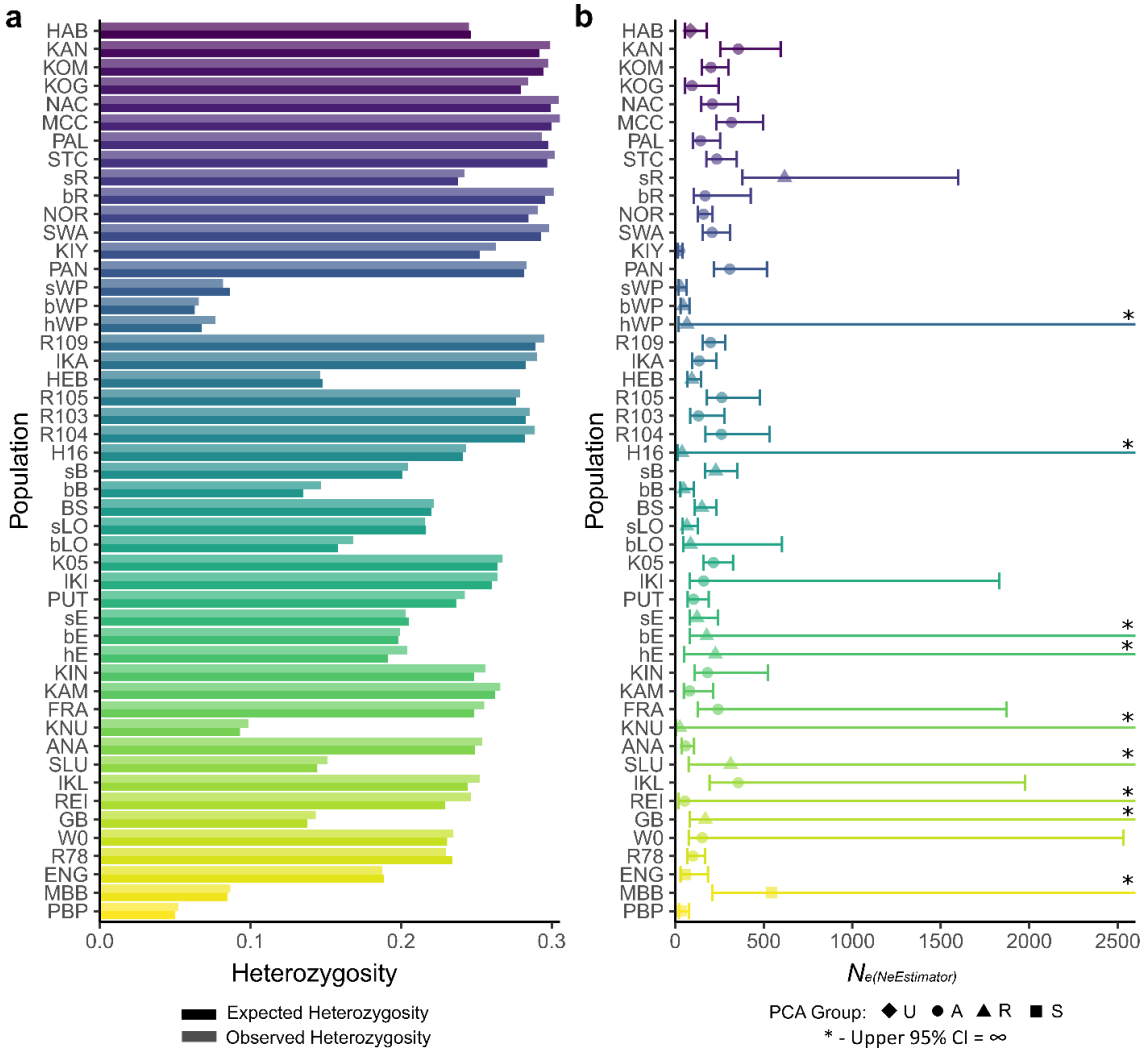

Fig.6.4 Genetic diversity estimates for 49 populations of Arctic Charr using putative neutral SNPs (N = 22259): a) observed and expected Heterozygosities and b) $\widehat{N}_{e(\text{NeEstimator})}$ with 95% jackknife confidence intervals. Shape of points for $\widehat{N}_{e(\text{NeEstimator})}$ indicate assigned PCA Group: Ungava (U), Northern Labrador Anadromous (A), Northern Labrador Resident/Landlocked (R), Southern Labrador and Newfoundland (S). Populations are ordered starting with the Ungava population (HAB) and then from north to south.

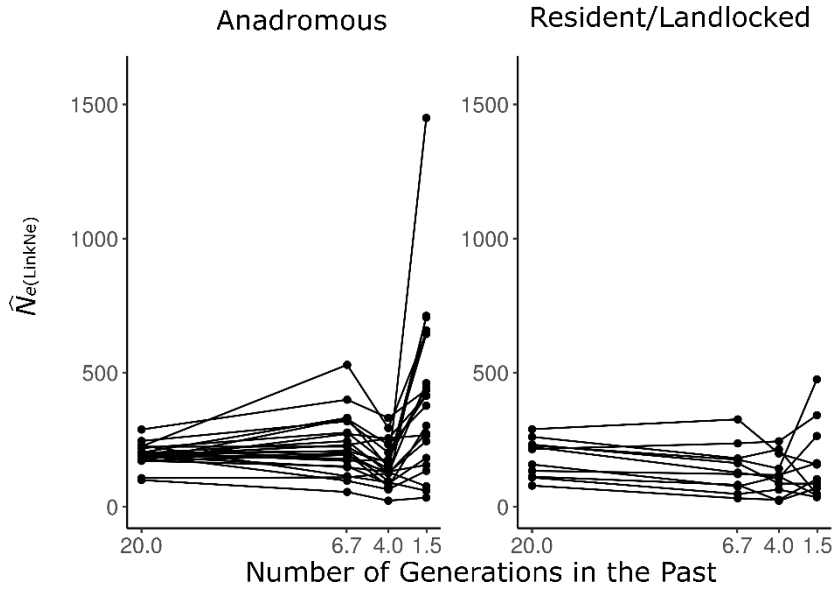

Fig.6.5 Results of LinkNe analysis for all Arctic Charr populations in northern Labrador with a non-infinite $\widehat{N}_{e(\text{LinkNe})}$ or upper 95% parametric confidence interval estimate for all four historical time points for which N_e was estimated.

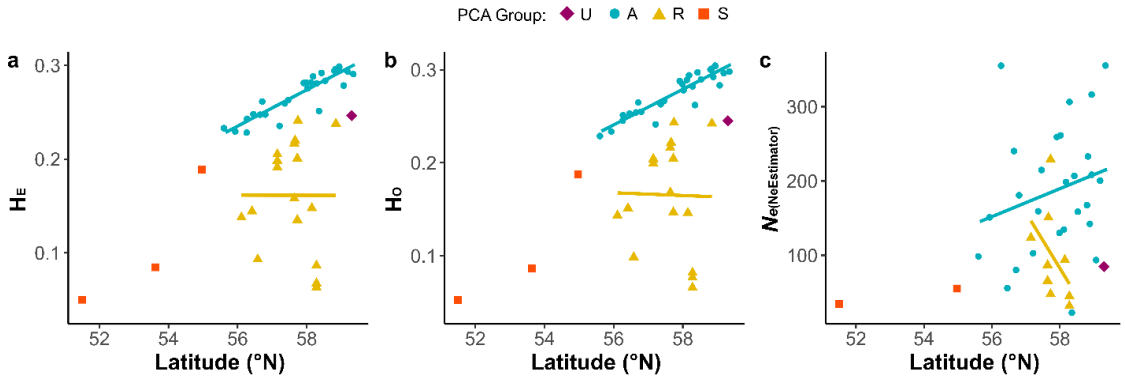

Fig.6.6 a) Expected Heterozygosity (H_E), b) Observed Heterozygosity (H_O), and c) $\widehat{N}_{e(\text{NEstimator})}$ estimates vs. latitude using N = 22259 putative neutral SNPs for Arctic Charr populations from four PCA Groups: Ungava (U), Northern Labrador Anadromous (A), Northern Labrador Resident/Landlocked (R), Southern Labrador and Newfoundland (S).

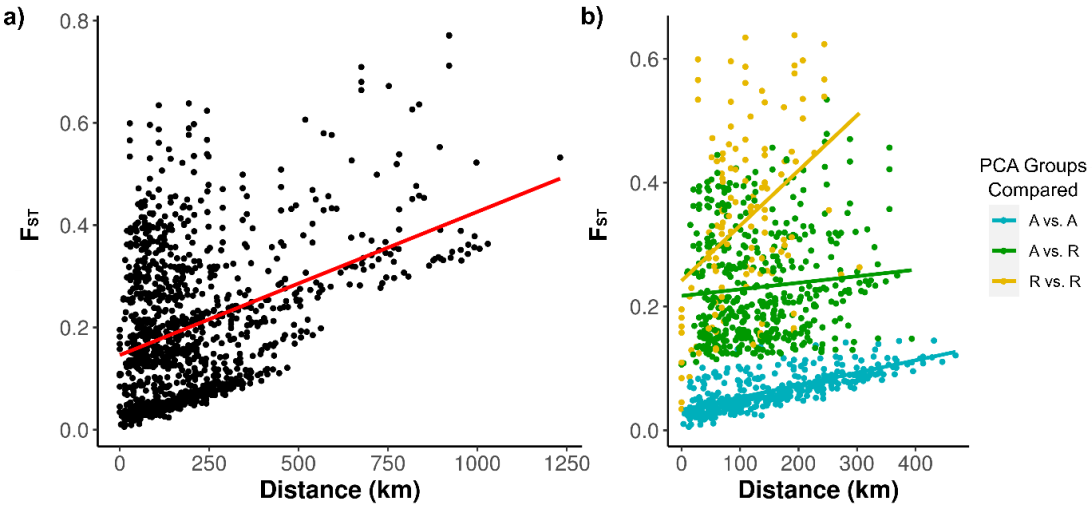

Fig.6.7 a) Pairwise F_{ST} (based on all SNPs, N = 22935) vs. Distance (km) between a) all 49 Arctic Charr populations, and between b) only those Arctic Charr populations (N = 45) in the Northern Labrador Anadromous (A), Northern Labrador Resident/Landlocked (R) PCA Groups.

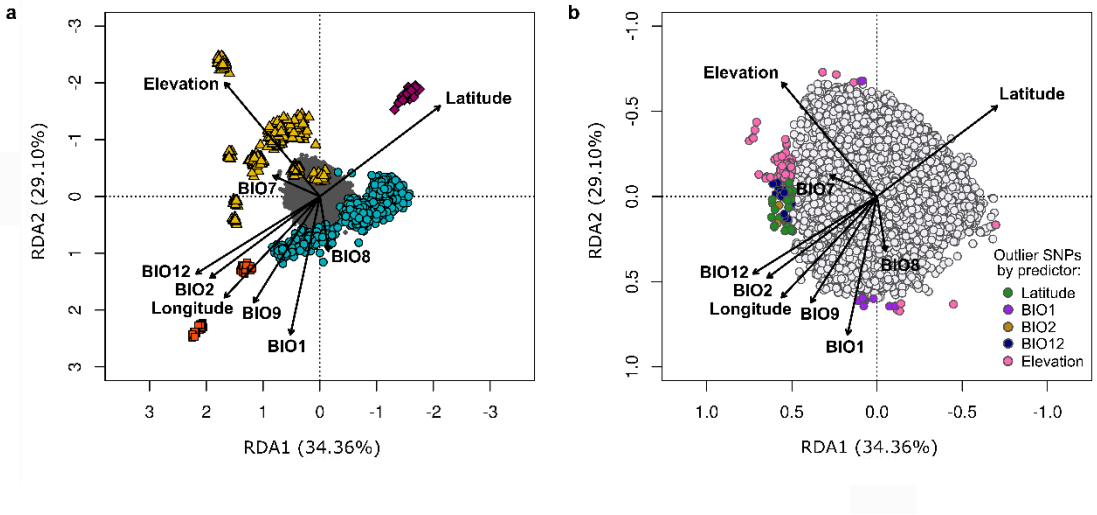

Fig.6.8 Results of RDA analysis for RDA1 vs. RDA2 testing the influence of 9 predictor variables on the genetic variation (N = 22935 SNPs) in 49 populations of Arctic Charr. The predictor variables include: Latitude, Longitude, BIO1 (Annual Mean Temperature), BIO2 (Mean Diurnal Range), BIO7 (Temperature Annual Range), BIO8 (Mean Temperature of Wettest Quarter), BIO9 (Mean Temperature of Driest Quarter), BIO12 (Annual Precipitation), and Elevation. a) loadings of 9 predictor variables in relation to 1206 Arctic Charr individuals grouped by PCA Group: Ungava (U), Northern Labrador Anadromous (A), Northern Labrador Resident/Landlocked (R), Southern Labrador and Newfoundland (S). b) loadings of 9 predictor variables in relation to 22935 SNPs. Outlier SNPs with loadings > 3 SD from the mean distribution of RDA1 and RDA2 are coloured by the predictor variable with which they most closely associate.

6.9 Supporting Information

6.9.1 Genetic Structure of W0 sites

Table S6.1 Cross-validation error for ADMIXTURE analyses of all individuals from W01, W02, W03 locations based on 20751 SNPs.

K	CV
1	0.59015
2	0.73644
3	0.89961
4	1.00302
5	1.26362

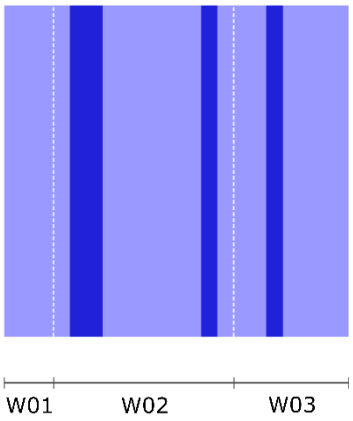

Fig.S6.1 Plot of K = 2 for ADMIXTURE analyses of all individuals from W01, W02, W03 locations based on 20751 SNPs.

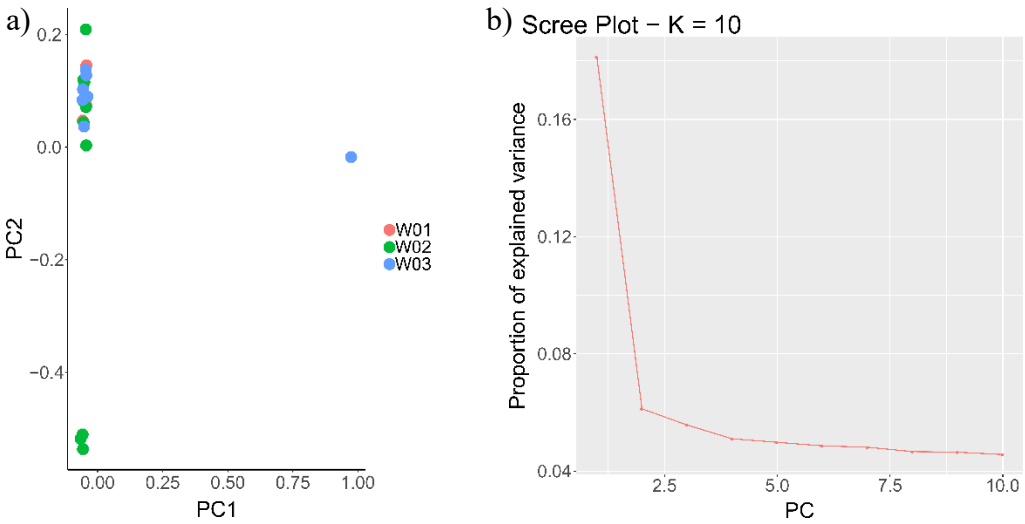

Fig.S6.2 Results of PCAdapt analyses of all individuals from W01, W02, W03 locations based on 20751 SNPs, testing K = 1-10 with the default Mahalanobis distance. a) Plot of PC1 vs. PC2. b) Screeplot of K = 1-10.

6.9.2 F_{ST} and IBD analyses using only putative neutral SNPs

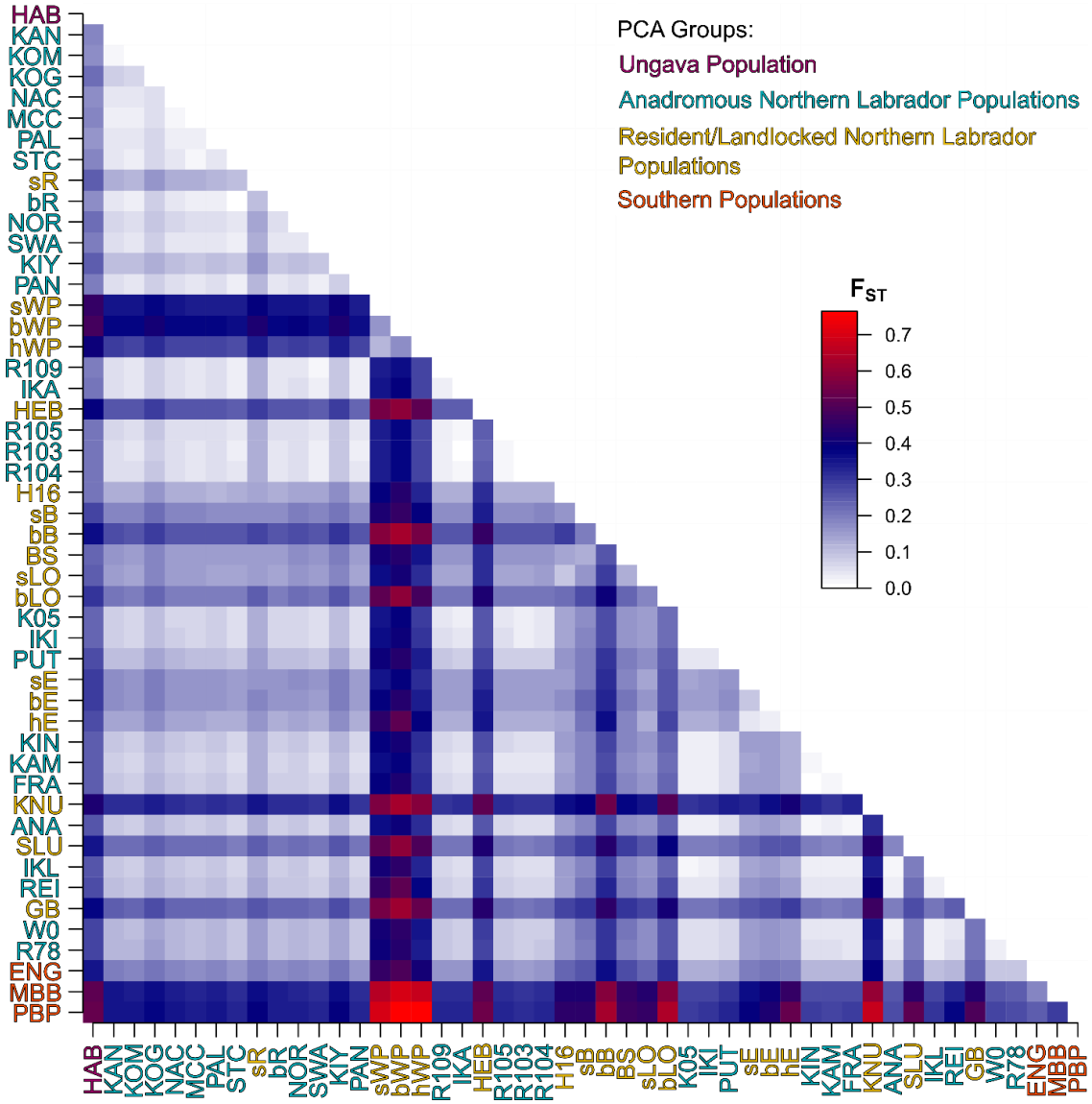

Fig.S6.3 Pairwise weighted Weir and Cockerham (1984) F_{ST}s between 49 populations of Arctic Charr using putative neutral SNPs (N = 22259). Population labels are coloured based on assigned PCA Group and ordered starting with the Ungava population (HAB) and then from north to south.

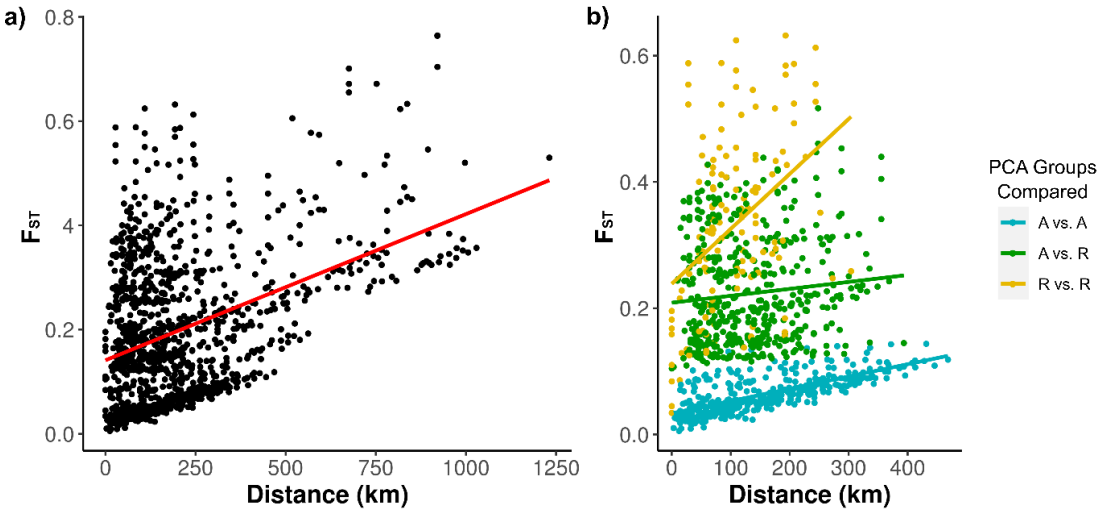

Fig.S6.4 a) Pairwise F_{ST} (based on putative neutral SNPs, N = 22259) vs. Distance (km) between a) all 49 Arctic Charr populations, and between b) only those Arctic Charr populations (N = 45) in the Northern Labrador Anadromous (A), Northern Labrador Resident/Landlocked (R) PCA Groups.

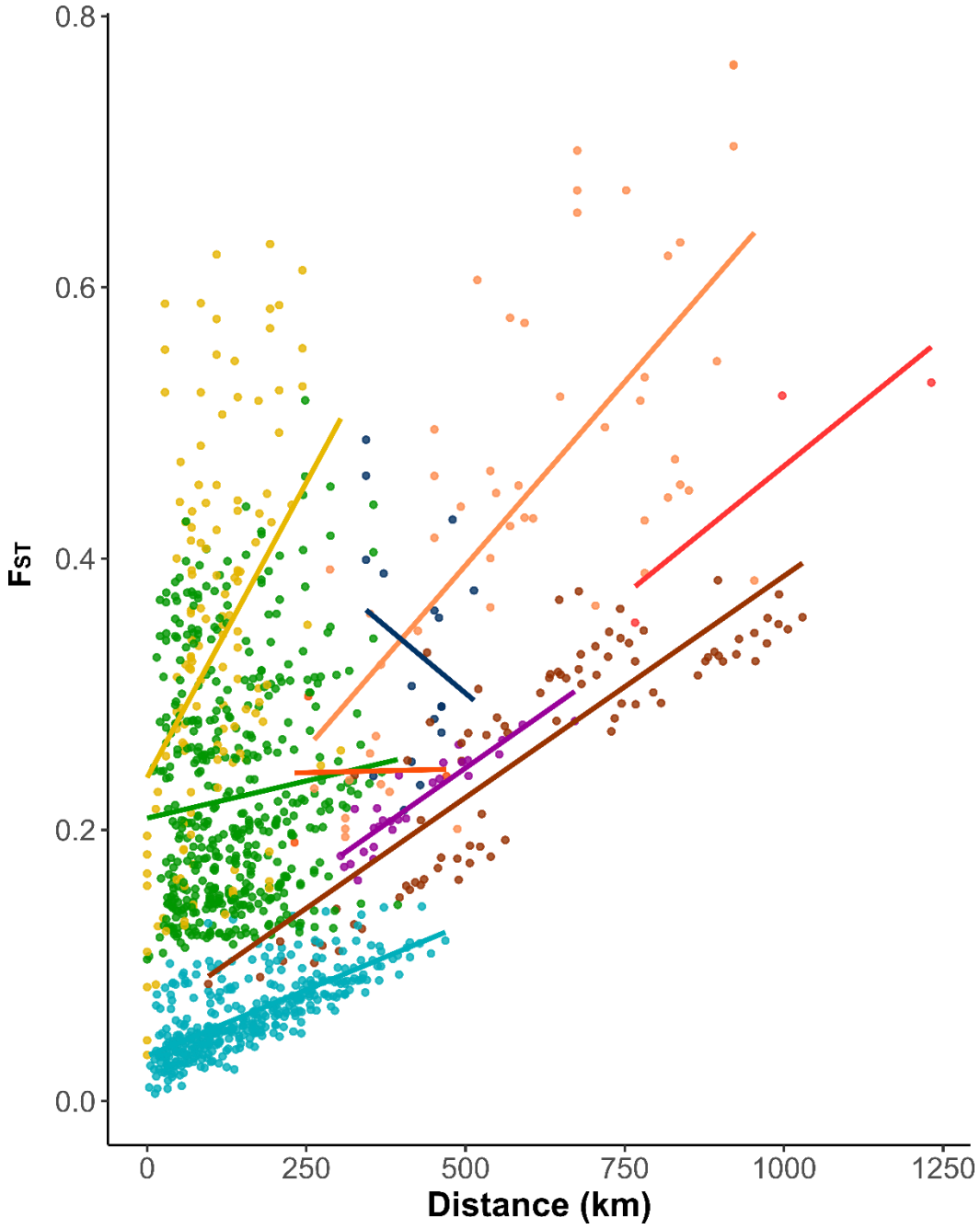

Fig.S6.5 F_{ST} (based on putative neutral N = 22259 SNPs) vs. distance (km) for all pairwise comparisons of populations. Comparisons are coloured by PCA Groups being compared.

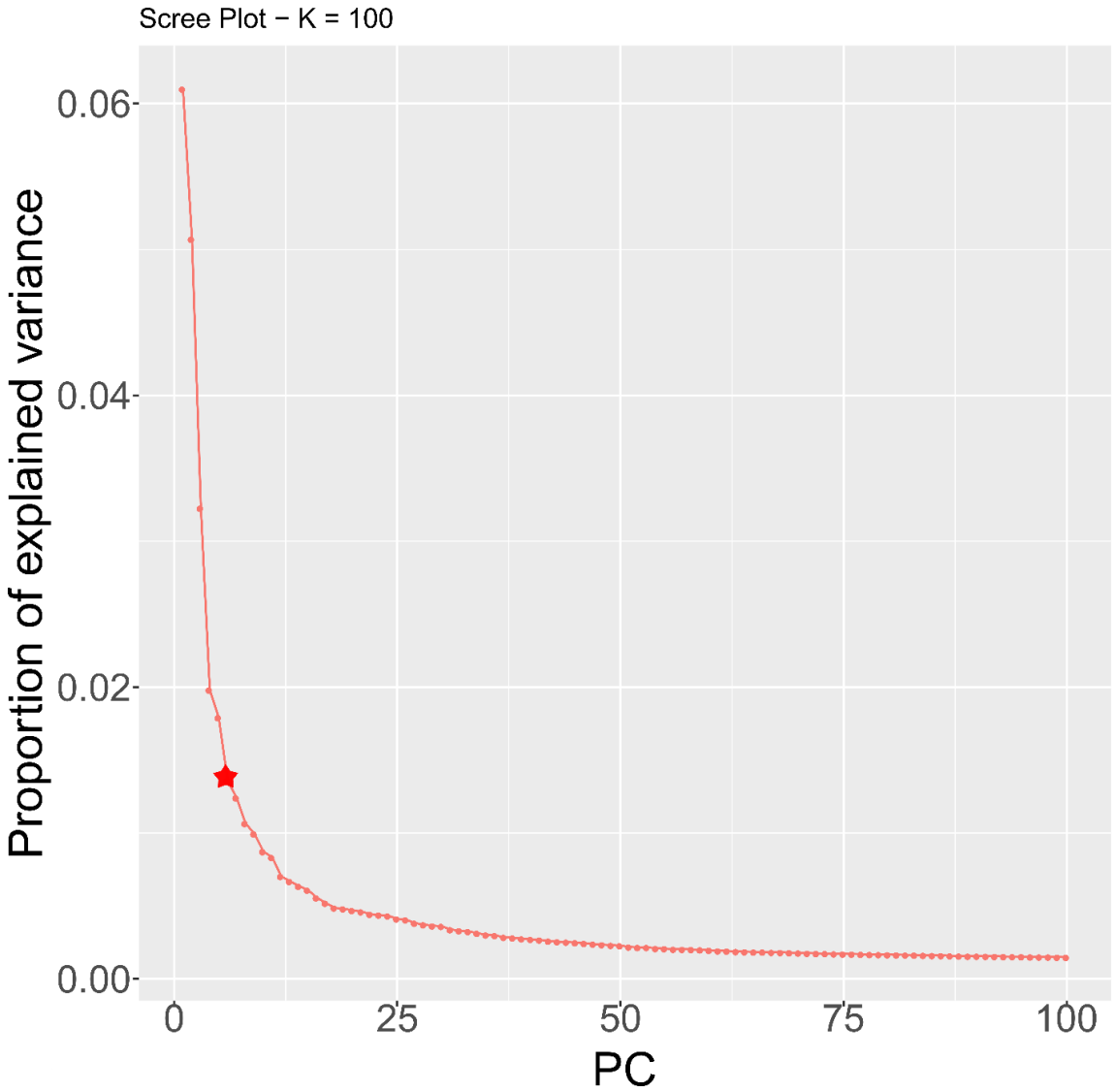

Fig.S6.6 Screeplot of PCAdapt analyses of all individuals from 49 populations based on 22935 SNPs, testing K = 1-100 with the default Mahalanobis distance. The starred PC is K=6, which was the number of PCs chosen for a reduced PCAdapt analysis to identify putative outlier loci.

6.9.3 Estimates of N_e using LinkNe and NeEstimator

Table S6.2 $\widehat{N}_e$ for all populations using NeEstimator ($\widehat{N}_{e(\text{NeEstimator})}$) and LinkNe ($\widehat{N}_{e(\text{LinkNe})}$) after applying a MAF cut-off of 0.05.

Population	N Individuals	N Loci	$\widehat{N}_{e(\text{NeEstimator})}$ (95% Jackknife CI)	$\widehat{N}_{e(\text{LinkNe})}$ (95% Parametric CI) 20 generations ago	$\widehat{N}_{e(\text{LinkNe})}$ (95% Parametric CI) 6.67 generations ago	$\widehat{N}_{e(\text{LinkNe})}$ (95% Parametric CI) 4 generations ago	$\widehat{N}_{e(\text{LinkNe})}$ (95% Parametric CI) 1.54 generations ago
HAB	29	725	85 (53.9-179.5)	228.47 (208.88-250.02)	110.77 (91.26-136.54)	99.78 (75.59-138.48)	118.7 (109.79-129.09)
KAN	30	890	356.8 (253.5-594.8)	198.72 (186.34-211.94)	419.18 (295.19-676.68)	339.21 (207.59-789.11)	8187.65 (1617.35--2699.16)
KOM	28	867	201.9 (151.3-300)	245.21 (228.03-263.85)	318.64 (234.5-471.99)	201.99 (138.31-343.42)	414.91 (336.34-540.28)
KOG	30	840	95 (56.7-244.2)	106.86 (101.42-112.53)	109.57 (94.26-128.43)	124.38 (95.42-170.54)	272.48 (237.39-319.32)
NAC	30	863	209.9 (147.7-354.9)	191.29 (179.53-203.81)	208.52 (166.19-270.71)	95.73 (76.99-122.41)	711.85 (520.6-1120.84)
MCC	30	898	317.7 (232.6-495.9)	230.56 (216.19-245.95)	265.09 (207.5-354.6)	184.18 (133.13-280.85)	2259.99 (1069.04--21162.65)
PAL	30	881	143.7 (98.9-253.3)	191.36 (179.49-204.02)	230.2 (182.32-301.97)	255.63 (169.49-469.65)	266.99 (234.58-309.45)
STC	30	914	234.4 (175.7-348.1)	224.97 (211.42-239.44)	529.13 (355.21-953.75)	293.51 (191.25-567.81)	648.25 (492.29-946.06)
sR	32	646	617.8 (380.1-1599.6)	284.34 (255.68-316.59)	561.03 (321.99-1581.07)	1642.45 (343.29--729.39)	7714.92 (1302.18--1988.27)
bR	28	894	168.9 (103.2-426.3)	171.45 (161.42-182.1)	192.95 (155.57-246.72)	124.48 (95.47-171.08)	460.82 (368.19-614.38)
NOR	30	868	160.1 (128.1-211.6)	174.27 (164.23-184.88)	271.78 (208.93-373.37)	253.98 (166.68-477.55)	413.95 (340.66-526.45)
SWA	30	899	208.3 (156.3-308.5)	201.92 (190.47-214.08)	331.45 (250.19-470.6)	147.2 (112.26-204.6)	706.24 (522.87-1083.58)
KIY	28	743	24.2 (15.9-41.3)	99.46 (93.31-105.94)	55.07 (47.86-63.51)	22.62 (19.85-25.79)	33.96 (33.07-34.9)
PAN	30	864	307.8 (217.7-517.4)	201.5 (188.83-215.04)	320.05 (237.53-466.27)	250 (165.82-458.38)	2454.59 (1086.28--9803.74)
sWP	28	254	31.9 (19.7-63.5)	157.57 (128.67-192.24)	75.53 (47.78-126.89)	113.15 (52.45-520.12)	42.54 (38.79-46.98)
bWP	24	189	45 (30.1-80.3)	78.78 (61.9-98.86)	31.64 (19.41-51.53)	25.67 (15.31-44.46)	103.19 (77.26-152.95)
hWP	6	201	66.9 (20.1-Infinite)	147.07 (84.75-327.33)	45.3 (15.19--184.01)	38.58 (9.48--44.08)	113.99 (38.86--129.82)
R109	30	896	200 (154.2-281.9)	199.79 (188.4-211.87)	207.47 (168.43-262.91)	167.79 (124.49-244.38)	644.12 (486.52-949.74)
IKA	25	821	136.1 (95.1-232.3)	182.91 (171.02-195.67)	199.07 (154.23-269.67)	74.67 (59.92-95.67)	302.7 (251.14-380.19)
HEB	30	424	93.9 (68.4-145.1)	133.85 (117.71-151.89)	121.79 (87.41-178.45)	118.16 (70.93-247.06)	162.73 (137.99-197.68)
R105	30	833	262.8 (179.6-478.8)	223.82 (209.62-239.01)	224.16 (176.49-296.23)	141.61 (106.73-200.07)	1449.69 (816.56-6301.24)
R103	29	867	131.6 (84.5-277)	199.24 (187.01-212.29)	244.82 (189.54-332.31)	126.99 (97.18-175.01)	244.23 (215.4-281.67)
R104	29	875	260.7 (170.8-532.9)	199.24 (187.42-211.82)	173.74 (141.95-217.89)	128.4 (98.59-176.23)	2504.57 (1076.19--7866.17)

Table S6.2 Continued.

Population	N Individuals	N Loci	$\widehat{N}_{e(\text{NeEstimator})}$ (95% Jackknife CI)	$\widehat{N}_{e(\text{LinkNe})}$ (95% Parametric CI) 20 generations ago	$\widehat{N}_{e(\text{LinkNe})}$ (95% Parametric CI) 6.67 generations ago	$\widehat{N}_{e(\text{LinkNe})}$ (95% Parametric CI) 4 generations ago	$\widehat{N}_{e(\text{LinkNe})}$ (95% Parametric CI) 1.54 generations ago
H16	18	678	38.6 (12-Infinite)	260.54 (228.52-298.71)	180.4 (122.08-309.3)	214.03 (107.71-1460.44)	46.74 (44.09-49.71)
sB	42	543	229.1 (168.5-351.2)	228.62 (206.19-253.28)	175.62 (135.85-233.77)	142.33 (100.68-217.67)	474.91 (372.19-653.27)
bB	16	393	47.8 (29.7-105)	112.18 (96.48-130.56)	81.73 (54.05-138.23)	22.3 (16.28-31.39)	69.86 (59.56-84.19)
BS	29	595	151 (111.2-231.1)	222.54 (199.63-248.22)	127.36 (98.77-169.44)	106.74 (75.74-163.57)	263.94 (218.09-333.33)
sLO	21	594	65.6 (42.9-128)	231.7 (204.3-263.61)	162.53 (113.27-259.28)	86.43 (59.56-140.24)	86.28 (78.23-96.08)
bLO	8	485	86.9 (45.5-603.4)	175.41 (135.64-236.6)	144.64 (61.93--1317.85)	59.45 (28.29-609.41)	130 (81.06-322.2)
K05	29	791	216.2 (160.7-326.2)	218.53 (203.58-234.61)	276.74 (203.25-408.56)	158.1 (113.54-242.58)	658.12 (474.72-1067.5)
IKI	27	783	160.7 (80.7-1831.7)	172.2 (160.47-184.78)	327.5 (226.95-541.22)	231.99 (146.63-478.81)	376.64 (302.85-496.77)
PUT	24	686	104.2 (70.6-189.3)	171.15 (157.12-186.45)	150.71 (114.49-208.44)	86.04 (64.18-122.29)	182.29 (157.74-215.55)
sE	33	577	123.6 (81.1-241.3)	289.23 (257.66-325.03)	325.75 (216.7-573.07)	198.56 (125.32-393.97)	157.4 (141.17-177.62)
bE	21	549	177.9 (82-Infinite)	215.01 (188.89-245.43)	236.36 (143.6-520.41)	244.09 (113.8-6509.85)	341.33 (240.92-580.43)
hE	6	574	227 (50.2-Infinite)	236.4 (168.67-370.21)	-388.97 (135.39--90.23)	76.4 (29.19--205.3)	122.07 (71.25-415.23)
KIN	24	712	182.2 (108.2-524.4)	202.43 (185.89-220.54)	171.18 (128.84-240.88)	176.45 (110.8-364.56)	444.14 (326.58-690.75)
KAM	29	776	81.7 (48.4-213)	192.36 (179.94-205.62)	96.88 (82.22-115.2)	64.55 (53.3-79.41)	133.98 (123.54-146.25)
FRA	23	676	241.7 (126.5-1871.5)	288.03 (255.76-325.52)	399.27 (232.86-1064.59)	331.14 (153.36-143707.59)	435.9 (314.24-707.4)
KNU	16	253	26.6 (6.5-Infinite)	108.85 (85.01-139.43)	47.58 (30.01-81.95)	63.87 (28.18-435.81)	36 (31.37-42.04)
ANA	30	730	57.3 (37.6-106.8)	188.14 (173.79-203.63)	147.47 (118.39-188.28)	129.33 (94.28-191.51)	76.52 (72.78-80.65)
SLU	10	450	313.4 (75.7-Infinite)	159.67 (129.86-199.99)	106.37 (56.45-378.66)	206.83 (50.89--143.07)	-2800.97 (302.86--252.25)
IKL	17	731	356.6 (193.9-1975.9)	226.47 (204.38-251.66)	230.92 (147.83-458.17)	-1212.41 (321.86--234.65)	4619.67 (729.42--1076.65)
REI	9	724	54.2 (17.7-Infinite)	228.2 (192.59-275.33)	114.01 (71.05-244.82)	91.09 (47.65-449.42)	59.59 (51.37-70.85)
GB	12	373	170.1 (82.4-Infinite)	129.27 (106.66-158.02)	157.75 (71.86-2507.02)	217.91 (54.37--165.69)	770.6 (208.85--467.65)
W0	21	642	152.5 (75.9-2530.3)	231.71 (207.57-259.22)	208.15 (140.26-358.71)	358.34 (149.03--1746.48)	265.26 (207.45-366.48)
R78	24	698	99.9 (69.9-168.9)	191.91 (175.45-210.05)	179.63 (132.74-260.38)	131.07 (90.34-216.34)	155.81 (137.57-179.4)
ENG	30	594	55.3 (29.9-185)	223.08 (200.38-248.47)	154.43 (117.17-212.25)	132.12 (90.6-216.45)	70.66 (66.73-75.05)

Table S6.2 Continued.

Population	N Individuals	N Loci	$\widehat{N}_{e(\text{NeEstimator})}$ (95% Jackknife CI)	$\widehat{N}_{e(\text{LinkNe})}$ (95% Parametric CI) 20 generations ago	$\widehat{N}_{e(\text{LinkNe})}$ (95% Parametric CI) 6.67 generations ago	$\widehat{N}_{e(\text{LinkNe})}$ (95% Parametric CI) 4 generations ago	$\widehat{N}_{e(\text{LinkNe})}$ (95% Parametric CI) 1.54 generations ago
MBB	26	207	542.9 (208.7-Infinite)	163.02 (120.16-221.4)	60.05 (34.65-111.59)	-3891.45 (94.42--146.25)	-838.3 (757.75--275.54)
PBP	15	150	34.2 (20.9-76.7)	79.68 (56.25-111.83)	20.86 (9.71-46.1)	24.11 (11.03-70.3)	60.86 (42.48-104.21)

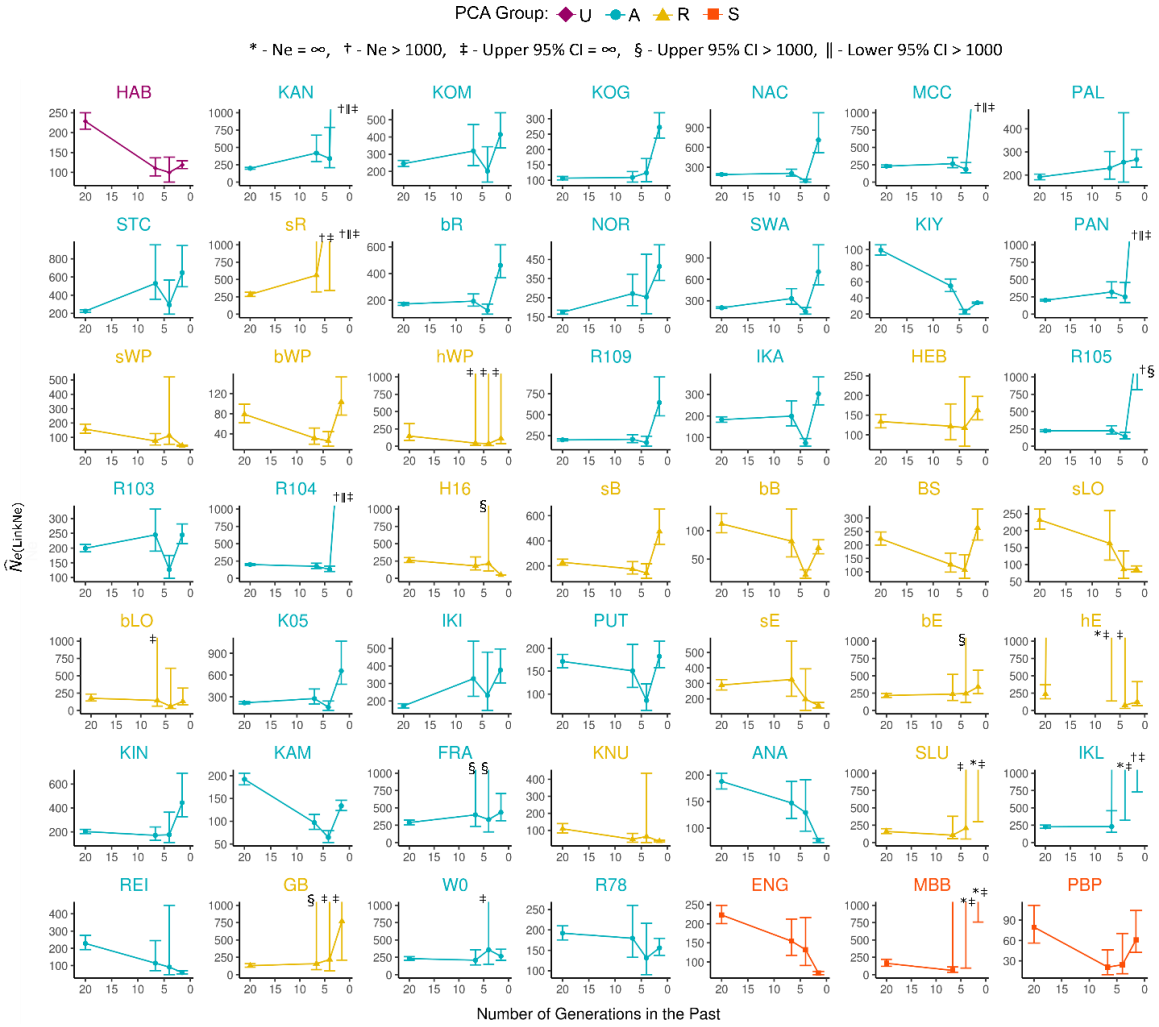

Fig.S6.7 LinkNe N_e estimates for four time points for all populations. Error bars represent 95% parametric confidence intervals. Colour indicates the PCA Group of each population: Ungava (U), Northern Labrador Anadromous (A), Northern Labrador Resident/Landlocked (R), Southern Labrador and Newfoundland (S).

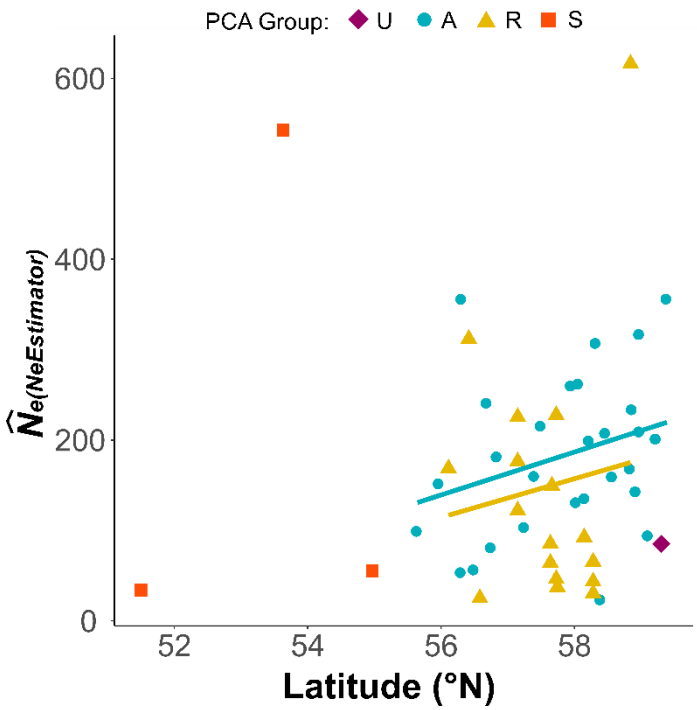

Fig.S6.8 Plot of $\widehat{N}_{e(\text{NeEstimator})}$ vs. latitude for all populations including those populations with an upper 95% CI of infinity and the high outlier $\widehat{N}_{e(\text{NeEstimator})}$ for sR.

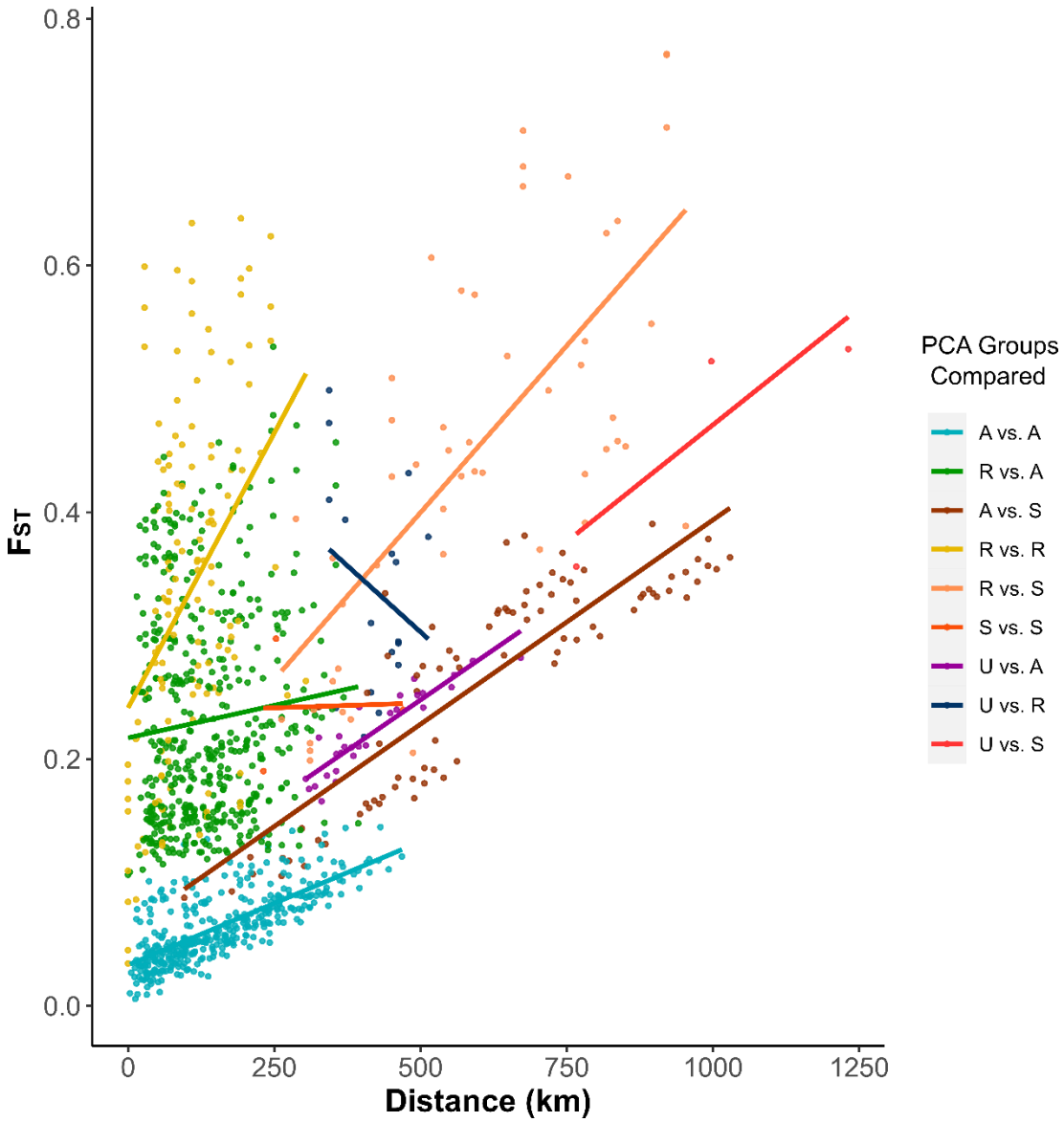

Fig.S6.9 F_{ST} (based on N = 22935 SNPs) vs. distance (km) for all pairwise comparisons of populations. Comparisons are coloured by PCA Groups being compared.

6.9.4 RDA Analyses

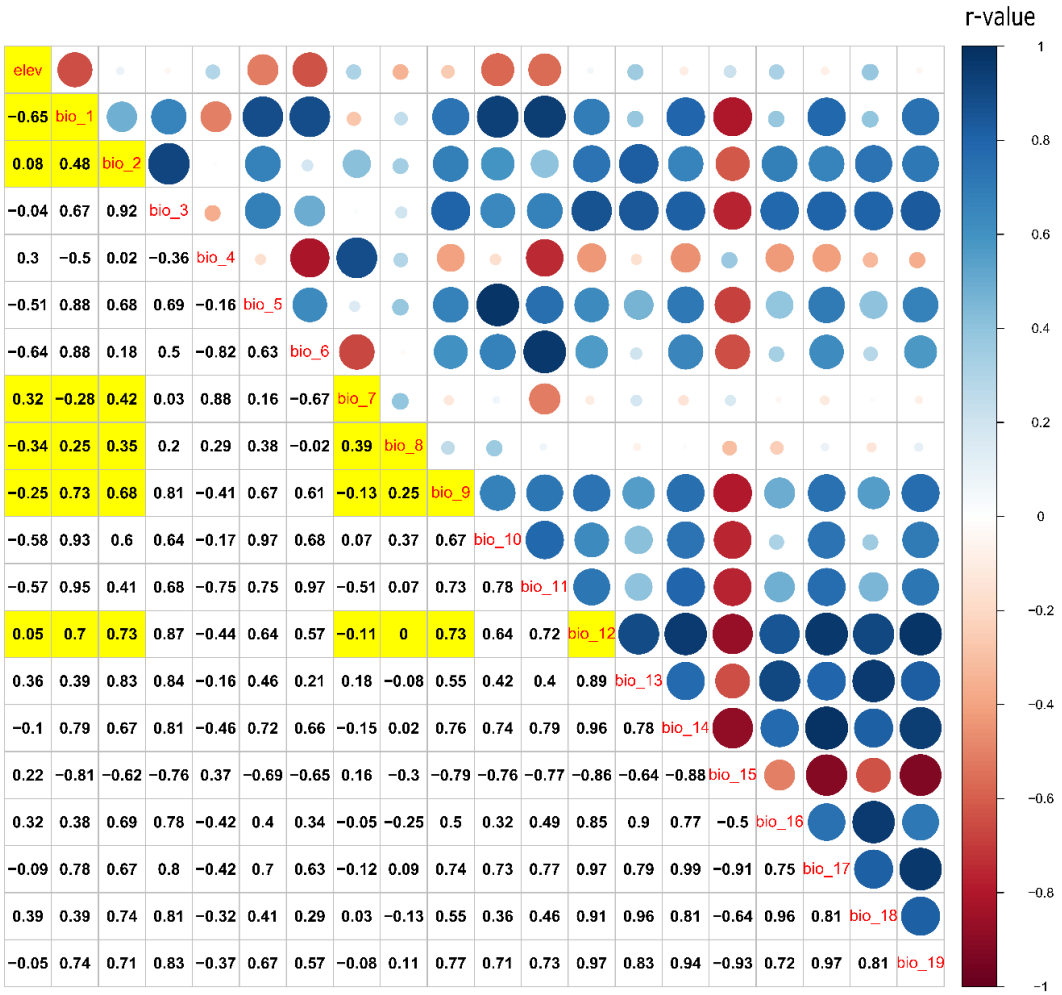

Fig.S6.10 Pearson correlation coefficients between all Bioclim and altitude variables from the World Clim database. Highlighted variables were those chosen for the final RDA and all of their Pearson correlation coefficients < 0.75 (highlighted). (elev – elevation, bio_1 – annual mean temperature, bio_2 – mean diurnal range, bio_3 – isothermality, bio_4 – temperature seasonality, bio_5 – max temperature of warmest month, bio_6 – min temperature coldest month, bio_7 temperature annual range, bio_8 mean temperature of wettest quarter, bio_9 – mean temperature of driest quarter, bio_10 – mean temperature of warmest quarter, bio_11 – mean temperature of coldest quarter, bio_12 – annual precipitation, bio_13 – precipitation of wettest month, bio_14 – precipitation of driest month, bio_15 – precipitation seasonality, bio_16 – precipitation of wettest quarter, bio_17 – precipitation of driest quarter, bio_18 – precipitation of warmest quarter, bio_19 – precipitation of coldest quarter)

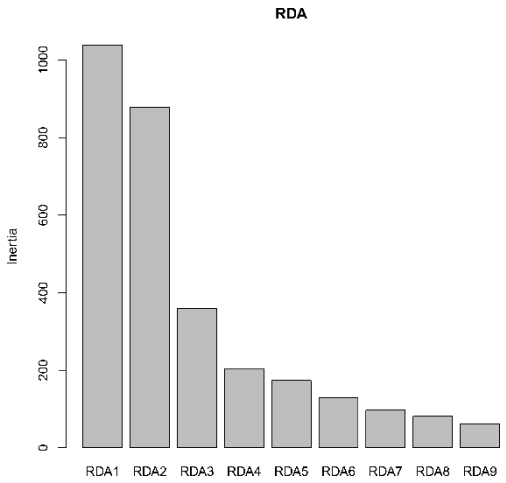

Fig.S6.11 Eigenvalues for each RDA loading contributing to the RDA analysis.

Table S6.3 Significance of each term in the RDA analysis after 999 permutations.

	Df	Variance	F	Pr(>F)
Longitude	1	812	48.7629	0.001
Latitude	1	448.8	26.9522	0.001
altS	1	873.4	52.4547	0.001
bio1	1	127.4	7.6491	0.001
bio2	1	228.4	13.7194	0.001
bio7	1	142.4	8.5499	0.001
bio8	1	170.2	10.2238	0.001
bio9	1	80.7	4.8456	0.001
bio12	1	137.1	8.2309	0.001
Residual	1196	19914.7		

Table S6.4 SNPs identified as outliers from RDA analysis.

SNP Code	Linkage Group	Absolute Position (bp)	Gene Name	Protein Code	SNP Position relative to CDS (bp)	RDA Axis	Predictor Variable most Associated with Outlier SNP	Detected as OL by PCAdapt	Detected as OL between 5/7 landlocked vs. anadromous pairs (Chapter 5)
AX-181984090	AC01	23560311	voltage-dependent L-type calcium channel subunit alpha-1D-like	XP_023840760.1	0	1	latlong.Lat		
AX-181985887	AC01	23621220	LOW QUALITY PROTEIN: voltage-dependent calcium channel subunit alpha-2/delta-3-like	XP_024002815.1	0	1	latlong.Lat	*	
AX-181944498	AC01	24840547	NA	NA	NA	1	elev		
AX-181915356	AC01	35411160	testis-expressed protein 264	XP_023846850.1	0	1	latlong.Lat		
AX-181989154	AC02	28226269	NA	NA	NA	2	elev	*	
AX-181966527	AC03	16506547	vinculin isoform X4	XP_023825639.1	0	2	bio_1		
AX-181927102	AC03	23286636	uncharacterized protein LOC111953042	XP_023827900.1	0	2	bio_1		
AX-181968250	AC04p	6300701	methylosome subunit pICln isoform X4	XP_023836980.1	0	1	latlong.Lat		
AX-181985502	AC04q1.29	6527392	fructose-1,6-bisphosphatase 1	XP_023839253.1	0	1	latlong.Lat		
AX-181934003	AC04q1.29	6528214	fructose-1,6-bisphosphatase 1	XP_023839253.1	0	1	latlong.Lat		
AX-181915569	AC05	27561879	transmembrane protein 164 isoform X2	XP_023843672.1	0	1	elev		
AX-181958554	AC06.1	14227893	NA	NA	NA	2	bio_1	*	
AX-181937410	AC06.1	15048474	sialic acid-binding Ig-like lectin 5	XP_023844980.1	0	2	elev	*	
AX-181932713	AC07	5477927	vesicular inhibitory amino acid transporter-like	XP_023846509.1	0	2	bio_1		
AX-181919997	AC07	12457572	forkhead box protein J3-like	XP_023846783.1	4343	1	latlong.Lat	*	
AX-181932135	AC07	13633808	troponin C, skeletal muscle-like	XP_023846825.1	0	1	bio_12	*	
AX-181937960	AC08	798438	LOW QUALITY PROTEIN: protocadherin-11 X-linked-like	XP_023847824.1	0	1	elev		*
AX-181959111	AC08	1002210	NA	NA	NA	1	elev		
AX-181914415	AC08	1035703	NA	NA	NA	1	elev		
AX-181933648	AC08	32946280	TBC1 domain family member 12 isoform X2	XP_023848860.1	0	1	elev	*	
AX-181933645	AC08	33118168	polycomb group RING finger protein 5-B isoform X2	XP_023848890.1	0	1	elev	*	
AX-181983747	AC08	33137376	ankyrin repeat domain-containing protein 1-like isoform X2	XP_023848881.1	0	1	elev	*	

Table S6.4 Continued.

SNP Code	Linkage Group	Absolute Position (bp)	Gene Name	Protein Code	SNP Position relative to CDS (bp)	RDA Axis	Predictor Variable most Associated with Outlier SNP	Detected as OL by PCAdapt	Detected as OL between 5/7 landlocked vs. anadromous pairs (Chapter 5)
AX-181933644	AC08	33140506	ankyrin repeat domain-containing protein 1-like isoform X2	XP_023848881.1	0	1	elev	*	
AX-181930400	AC08	38876676	ras-interacting protein 1-like	XP_023849558.1	0	1	elev		
AX-181925901	AC08	38877902	ras-interacting protein 1-like	XP_023849558.1	0	1	elev		
AX-181914426	AC08	38938285	canalicular multispecific organic anion transporter 2 isoform X4	XP_023849063.1	0	1	elev		
AX-181970666	AC08	41811428	NA	NA	NA	1	elev		
AX-181983108	AC10	7026046	uncharacterized protein LOC111969224	XP_023850995.1	0	1	elev		
AX-181942417	AC11	30234144	NA	NA	NA	2	elev	*	
AX-181984892	AC11	47025011	acid-sensing ion channel 1-like	XP_023853047.1	0	1	elev		
AX-177653991	AC13	38276850	protein ABHD8	XP_023853950.1	-6	1	elev		
AX-181975052	AC13	38282403	NA	NA	NA	1	elev		
AX-181944529	AC13	38449597	retinal rod rhodopsin-sensitive cGMP 3',5'-cyclic phosphodiesterase subunit delta	XP_023853958.1	0	1	elev		
AX-181944552	AC13	38449757	retinal rod rhodopsin-sensitive cGMP 3',5'-cyclic phosphodiesterase subunit delta	XP_023853958.1	0	1	elev		
AX-181963925	AC13	38562499	prothymosin alpha isoform X1	XP_023853964.1	0	1	elev		
AX-181940100	AC13	42666767	microsomal triglyceride transfer protein	XP_023854103.1	0	1	elev		
AX-182162948	AC13	42985778	NA	NA	NA	1	elev		
AX-181926963	AC13	43157205	ADP/ATP translocase 1	XP_023854121.1	0	1	latlong.Lat		
AX-181926964	AC13	43157490	ADP/ATP translocase 1	XP_023854121.1	0	1	latlong.Lat		
AX-181974848	AC13	43277290	NA	NA	NA	1	latlong.Lat		
AX-181918763	AC13	43293438	NA	NA	NA	1	latlong.Lat		
AX-181965187	AC13	43293497	NA	NA	NA	1	latlong.Lat		
AX-181918876	AC13	43315665	microtubule-associated protein 9	XP_023854125.1	0	1	latlong.Lat		

Table S6.4 Continued.

SNP Code	Linkage Group	Absolute Position (bp)	Gene Name	Protein Code	SNP Position relative to CDS (bp)	RDA Axis	Predictor Variable most Associated with Outlier SNP	Detected as OL by PCAdapt	Detected as OL between 5/7 landlocked vs. anadromous pairs (Chapter 5)
AX-181918981	AC13	43317525	microtubule-associated protein 9	XP_023854125.1	0	1	latlong.Lat		
AX-181989776	AC13	43317608	microtubule-associated protein 9	XP_023854125.1	0	1	latlong.Lat		
AX-181965188	AC13	43317648	microtubule-associated protein 9	XP_023854125.1	0	1	latlong.Lat		
AX-181919099	AC13	43381216	guanylate cyclase soluble subunit alpha-3	XP_023854128.1	0	1	latlong.Lat		
AX-181919189	AC13	43381428	guanylate cyclase soluble subunit alpha-3	XP_023854128.1	0	1	latlong.Lat		
AX-181919279	AC13	43482545	inactive ubiquitin carboxyl-terminal hydrolase 53-like	XP_023853807.2	0	1	latlong.Lat		
AX-182161370	AC13	43482759	inactive ubiquitin carboxyl-terminal hydrolase 53-like	XP_023853807.2	0	1	latlong.Lat		
AX-181961225	AC13	43657795	uncharacterized protein LOC111971273	XP_023853809.1	2529	1	latlong.Lat		
AX-181915502	AC14	14572412	NA	NA	NA	1	latlong.Lat		
AX-181944192	AC14	50014747	NA	NA	NA	1	latlong.Lat		
AX-181975526	AC15	22520669	trans-Golgi network integral membrane protein 2 isoform X1	XP_023857798.1	0	1	bio_2		
AX-181954878	AC15	52312900	adhesion G-protein coupled receptor G5 isoform X1	XP_023858347.1	0	2	bio_1		
AX-181941972	AC16	6438103	growth hormone-releasing hormone receptor-like	XP_023859436.1	0	1	latlong.Lat	*	
AX-181916308	AC17	22616133	partner of Y14 and mago B	XP_023861958.1	98	2	bio_1		*
AX-181916309	AC17	22616560	partner of Y14 and mago B	XP_023861958.1	0	2	elev		*
AX-181980622	AC17	22869580	LOW QUALITY PROTEIN: serine/threonine-protein phosphatase 6 regulatory ankyrin repeat subunit C-like	XP_023862177.1	2738	2	bio_1		*
AX-181983398	AC17	22869600	LOW QUALITY PROTEIN: serine/threonine-protein phosphatase 6 regulatory ankyrin repeat subunit C-like	XP_023862177.1	2718	2	bio_1		*
AX-181987181	AC17	22950203	inactive dipeptidyl peptidase 10	XP_023860785.1	0	2	elev		*
AX-181989947	AC18	34777418	potassium channel subfamily K member 18	XP_023862751.1	0	2	bio_1		
AX-181941976	AC18	42159349	uncharacterized protein LOC111978786 isoform X1	XP_023864794.1	-1346	1	latlong.Lat		
AX-181941975	AC18	42159384	uncharacterized protein LOC111978786 isoform X1	XP_023864794.1	-1381	1	latlong.Lat		

Table S6.4 Continued.

SNP Code	Linkage Group	Absolute Position (bp)	Gene Name	Protein Code	SNP Position relative to CDS (bp)	RDA Axis	Predictor Variable most Associated with Outlier SNP	Detected as OL by PCAdapt	Detected as OL between 5/7 landlocked vs. anadromous pairs (Chapter 5)
AX-181944390	AC18	67299855	NA	NA	NA	1	elev		
AX-181984368	AC19	9081631	nucleolar protein 9	XP_023865948.1	0	1	latlong.Lat		
AX-181992296	AC19	9082594	nucleolar protein 9	XP_023865948.1	0	1	latlong.Lat		
AX-182168667	AC19	23328979	laminin subunit gamma-2	XP_023865822.1	0	1	elev		
AX-182170259	AC20	6382929	LOW QUALITY PROTEIN: contactin-associated protein 1-like	XP_023868365.1	0	1	elev	*	
AX-181929388	AC20	44211923	dolichyl-diphosphooligosaccharide--protein glycosyltransferase subunit STT3A isoform X2	XP_023868868.1	0	1	elev		
AX-181942702	AC20	44241552	NA	NA	NA	1	elev		
AX-181929387	AC20	44254223	spectrin beta chain, non-erythrocytic 4-like	XP_023866672.1	0	1	elev	*	
AX-181973095	AC21	1423711	calpain-9	XP_023869744.1	0	1	elev	*	*
AX-181936535	AC21	1518313	uncharacterized protein LOC111982472	XP_023869810.1	0	1	elev	*	*
AX-181973093	AC21	1549701	myomesin-2	XP_024003594.1	0	1	elev	*	*
AX-181936531	AC21	1560037	myomesin-2	XP_024003594.1	-1756	1	elev	*	*
AX-181936530	AC21	1565479	LOW QUALITY PROTEIN: lengsin	XP_023869550.1	838	1	elev	*	*
AX-181967650	AC23	3204274	homeobox protein MSX-2	XP_023824809.1	0	2	elev	*	
AX-182166712	AC23	17461732	neural cell adhesion molecule 1-like isoform X1	XP_023824011.1	0	1	latlong.Lat		
AX-181935587	AC23	17781952	G protein-activated inward rectifier potassium channel 3	XP_023823364.1	0	1	latlong.Lat		
AX-181935586	AC23	17782342	G protein-activated inward rectifier potassium channel 3	XP_023823364.1	0	1	latlong.Lat		
AX-181935580	AC23	18062433	frizzled-9	XP_023824793.1	0	1	bio_12		
AX-181914573	AC23	18109883	NA	NA	NA	1	bio_12		
AX-181914186	AC23	18545710	NA	NA	NA	1	bio_12		
AX-181968270	AC23	18586808	NA	NA	NA	1	bio_12		
AX-181941544	AC23	18641530	LOW QUALITY PROTEIN: transcriptional regulator Erg-like	XP_023823705.1	0	1	latlong.Lat	*	

Table S6.4 Continued.

SNP Code	Linkage Group	Absolute Position (bp)	Gene Name	Protein Code	SNP Position relative to CDS (bp)	RDA Axis	Predictor Variable most Associated with Outlier SNP	Detected as OL by PCAdapt	Detected as OL between 5/7 landlocked vs. anadromous pairs (Chapter 5)
AX-181933016	AC23	18721064	protein C-ets-2	XP_023824402.1	0	1	latlong.Lat	*	
AX-181941518	AC23	18796157	uroplakin-3b	XP_023824398.1	0	1	bio_12		
AX-181933441	AC23	19187273	alpha-ketoglutarate-dependent dioxygenase alkB homolog 4	XP_023824731.1	0	1	latlong.Lat	*	
AX-181933438	AC23	19272943	peroxisome assembly protein 12	XP_023824703.1	0	1	elev		*
AX-181933437	AC23	19419599	spindle and kinetochore-associated protein 2 isoform X1	XP_023823986.1	0	1	elev		
AX-181933434	AC23	19698413	exonuclease V-like isoform X2	XP_023823204.1	0	1	elev		*
AX-182165632	AC23	20027708	collagen alpha-1(XXVI) chain-like	XP_023823891.1	-3226	1	elev		*
AX-181941388	AC23	20030524	matrix metalloproteinase-28-like	XP_023823338.1	2901	1	elev		
AX-181966356	AC23	25187775	52 kDa repressor of the inhibitor of the protein kinase	XP_023824500.1	0	1	bio_12		
AX-181930497	AC23	25202036	cytoskeleton-associated protein 2 isoform X8	XP_023824346.1	0	1	bio_12		
AX-181977961	AC23	25202435	cytoskeleton-associated protein 2 isoform X8	XP_023824346.1	0	1	bio_12		
AX-181930493	AC23	25218590	dolichyl-diphosphooligosaccharide--protein glycosyltransferase subunit STT3A	XP_023823759.1	0	1	bio_12		
AX-181933265	AC25	25836978	eukaryotic translation initiation factor 4E-like isoform X1	XP_023826078.1	0	2	bio_1	*	
AX-181933266	AC25	25896253	cell division cycle and apoptosis regulator protein 1	XP_023990352.1	0	2	bio_1	*	
AX-181941507	AC26	43434089	NA	NA	NA	1	bio_12		
AX-181914811	AC27	3951611	NA	NA	NA	1	bio_12		
AX-181980572	AC28	21105992	transcription initiation factor IIA subunit 1 isoform X4	XP_023829486.1	0	1	bio_12		
AX-181957276	AC28	21298515	NA	NA	NA	1	bio_12		
AX-181942707	AC30	10740771	NA	NA	NA	1	latlong.Lat		
AX-181989831	AC31	27055050	engulfment and cell motility protein 1 isoform X2	XP_023831960.1	0	1	elev		
AX-181944793	AC32	31201361	HORMA domain-containing protein 1 isoform X1	XP_023832975.1	0	1	bio_12	*	
AX-181943113	AC32	32779992	protein ABHD4 isoform X2	XP_023832803.1	1145	1	bio_12	*	

Table S6.4 Continued.

SNP Code	Linkage Group	Absolute Position (bp)	Gene Name	Protein Code	SNP Position relative to CDS (bp)	RDA Axis	Predictor Variable most Associated with Outlier SNP	Detected as OL by PCAdapt	Detected as OL between 5/7 landlocked vs. anadromous pairs (Chapter 5)
AX-181987304	AC32	33083723	NA	NA	NA	1	bio_12	*	
AX-181935982	AC32	33091779	protocadherin-8-like	XP_023833692.1	0	1	bio_12	*	
AX-181935696	AC33	6177438	transmembrane protein 161B	XP_023834928.1	0	1	elev		
AX-181941948	AC33	18181765	transcription factor 7-like 1-A isoform X4	XP_023834568.1	0	1	bio_12		
AX-181953748	AC33	18287576	uncharacterized protein LOC112067917 isoform X3	XP_023990579.1	0	1	bio_12		
AX-181944756	AC33	18997336	phosphatidylinositol transfer protein beta isoform isoform X1	XP_023834100.1	0	1	latlong.Lat		
AX-181979711	AC33	19616533	rab5 GDP/GTP exchange factor isoform X2	XP_023834725.1	0	1	latlong.Lat		
AX-181971519	AC33	19717007	leucine-rich repeat-containing protein 43	XP_023834989.1	1867	1	latlong.Lat		
AX-181991169	AC33	19780186	CAP-Gly domain-containing linker protein 1 isoform X3	XP_023834974.1	0	1	latlong.Lat		
AX-181956377	AC33	20769576	oxysterol-binding protein 2 isoform X1	XP_023834320.1	0	1	latlong.Lat		
AX-181932607	AC33	20966512	NA	NA	NA	1	latlong.Lat		
AX-181953161	AC33	21405945	WSC domain-containing protein 2 isoform X1	XP_023835036.1	0	1	latlong.Lat		
AX-181915606	AC36	14568642	protocadherin-17	XP_023836560.1	-2504	1	bio_2		
AX-181930426	AC36	33298180	protein disulfide-isomerase A5	XP_023836750.1	0	2	elev		
AX-181962102	NW_019942552.1	1024443	NA	NA	NA	1	elev		
AX-181962130	NW_019942557.1	884025	NA	NA	NA	2	bio_1		
AX-181942930	NW_019942680.1	346611	NA	NA	NA	1	bio_12		
AX-181940969	NW_019943053.1	49880	ras-related protein Rap-2a-like	XP_023994763.1	-953	1	elev		
AX-181942357	NW_019943053.1	49940	ras-related protein Rap-2a-like	XP_023994763.1	-1013	1	elev		
AX-181927436	NW_019943149.1	153938	zinc-binding protein A33-like	XP_023995110.1	0	1	elev	*	
AX-181959488	NW_019943184.1	222061	NA	NA	NA	1	bio_12		
AX-181937222	NW_019943289.1	72441	negative elongation factor A-like isoform X1	XP_023995623.1	0	1	bio_12		

Table S6.4 Continued.

SNP Code	Linkage Group	Absolute Position (bp)	Gene Name	Protein Code	SNP Position relative to CDS (bp)	RDA Axis	Predictor Variable most Associated with Outlier SNP	Detected as OL by PCAdapt	Detected as OL between 5/7 landlocked vs. anadromous pairs (Chapter 5)
AX-182163829	NW_019943331.1	180099	LOW QUALITY PROTEIN: protein FAM193B	XP_023995767.1	0	1	elev		
AX-181915376	NW_019943349.1	37992	cullin-5-like isoform X2	XP_023995829.1	0	1	elev		
AX-181988974	NW_019943349.1	62678	PHD finger protein 13-like	XP_023995833.1	0	1	elev		
AX-181961614	NW_019943987.1	5301	GRAM domain-containing protein 2A-like	XP_023997478.1	0	1	elev		
AX-181986311	NW_019944038.1	249	E3 ubiquitin-protein ligase TRIM9-like	XP_023997536.1	0	1	bio_12		
AX-182172560	NW_019944415.1	33875	LOW QUALITY PROTEIN: nuclear receptor coactivator 2-like	XP_023998163.1	0	2	bio_1		
AX-181973991	NW_019945333.1	708	NA	NA	NA	1	bio_12		
AX-181967799	NW_019945591.1	37703	early growth response protein 4-like	XP_023999487.1	0	1	elev		
AX-181953226	NW_019946680.1	8627	NA	NA	NA	1	elev		
AX-181963219	NW_019947513.1	661	NA	NA	NA	1	elev		
AX-181962936	NW_019947616.1	14251	NA	NA	NA	1	elev		
AX-181915110	NW_019948763.1	7986	lens epithelial cell protein LEP503-like	XP_024001037.1	-880	1	elev		
AX-181952652	NW_019951681.1	8144	uncharacterized protein LOC112079941	XP_024001508.1	0	1	elev		
AX-181948280	NW_019957233.1	144	NA	NA	NA	1	bio_12		

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CHAPTER 7 - GENETIC CAUSES AND CONSEQUENCES OF SYMPATRIC MORPH DIVERGENCE IN SALMONIDAE: A SEARCH FOR MECHANISMS

7.1 Abstract

Because the genetic signatures of speciation can be erased by subsequent selection and drift, uncovering the genomic mechanisms of incipient speciation can be challenging. One way to overcome this issue is to study the genetic characteristics of recently evolved sympatric morphs demonstrating consistent phenotypic differences across multiple replicate populations. Such morphs are frequently observed in Salmonidae and provide natural replicates of incipient speciation that can be used to uncover the repeatability of speciation. Understanding how sympatric morphs evolve is critical to the conservation of their diversity; the loss of which could have significant ecological and economical consequences. Our review suggests that genetic differentiation among sympatric morphs is largely non-parallel but for a few key genes that are potentially critical to morph manifestation. Both glacial history and contemporary selective pressures can temper this differentiation. Our synthesis reveals salmonids to be a useful model for studying speciation and poses additional research questions to be answered by future study of this family.

7.2 Introduction

Since Darwin, the mechanism of speciation, that "mystery of mysteries" (Darwin 1859), has proven enduringly elusive. A genomic understanding of speciation has been thwarted by the erasure of genomic signatures of ancient incipient speciation by subsequent selection and drift (Bush 1994; Coyne and Orr 2004; Elmer and Meyer 2011). The study of recent radiations in species such as cichlids (Wagner et al. 2013; Brawand et al. 2015; McGee et al. 2016), Darwin's finches (Zhang et al. 2014; Lamichhaney et al. 2015), and *Heliconius* butterflies (Martin et al. 2013; Kozak et al. 2015) have therefore been instrumental in uncovering the genomics of speciation.

However, questions about the mechanism of speciation remain unanswered. For instance, how and over what temporal and spatial scales genetic differences accumulate among incipient species remains generally unanswered. The importance of genomic architecture, including which and how many regions of the genome are involved in

differentiation, remains undetermined (Rogers et al. 2013; Campbell et al. 2018). Recent studies have suggested large-scale chromosomal rearrangements may drive adaptive divergence (Berg et al. 2016; Jay et al. 2018; Kess et al. 2019; Lehnert et al. 2019a), but their importance to incipient speciation is unknown in comparison to smaller islands of genomic divergence (Wolf and Ellegren 2017). The repeatability of genomic differentiation, if we were to replay Gould's (1989) "tape" of life, is also an unanswered question (Blount et al. 2018). Though Gould (1989) advocated for the importance of contingency, evidence for parallel evolution has been increasingly observed (Elmer and Meyer 2011; Blount et al. 2018). Historical allopatry and subsequent secondary contact can also fuel later radiations (e.g., Feder et al. 2003; Meier et al. 2017; Lamichhaney et al. 2018); however, the prevalence of this process is unknown. Many species were separated into multiple distinct refugia during the Pleistocene the descendants of which having sometimes recently come into secondary contact (Hewitt 1996, 2000; Bernatchez and Wilson 1998). These historical processes directly dictate the genetic variation present in contemporary populations and could therefore have pervasive effects on incipient speciation. In addition to historical processes, a greater understanding of the contemporary factors driving genomic differentiation among incipient species is also needed to predict how differentiation will proceed into the future (Rundle and Nosil 2005). Investigating the mechanisms of speciation requires the comparison of multiple radiations. Ideally, these radiations should be evolutionarily independent, with minimal contemporary gene flow (Schluter 1996b) but also be closely related to ensure a similar genetic starting point prior to speciation (Elmer and Meyer 2011). Such requirements are fulfilled in isolated populations containing sympatric morphs (Schluter 1996a, 1996b).

Salmonidae is a family of fishes that has been noted for its extensive intraspecific phenotypic diversity. Much of this diversity has evolved recently, subsequent to their recolonization of deglaciated regions after the last glacial maximum 8000 – 40000 years ago (Behnke 1972). Some of this phenotypic variation occurs in sympatry in the form of phenotypically, ecologically, or genetically differentiated morphs which can be repeatably observed in multiple distinct locations (Taylor 1999). The source of the radiative capacity of salmonid species is unknown but may be due to an increase in genetic variation as a result of the whole genome duplication at the base of this clade 88 -

102 mya (Macqueen and Johnston 2014). The repeated, recent evolution of consistently differentiated sympatric morphs in the Salmonidae family of fishes could therefore represent a unique opportunity to study the genomic mechanisms of speciation (Schluter and McPhail 1993; Robinson and Wilson 1994; Schluter 1996b; Taylor 1999). However, only recent advances in sequencing technologies have allowed the assessment of the neutral and particularly of the adaptive genomic differentiation among morphs (Seehausen et al. 2014). The limited number of markers employed in early studies may have failed to detect real genetic differences among morphs (Jorde et al. 2018). Increased sequencing power and the development of multiple reference genomes within Salmonidae (e.g., Sutherland et al. 2016; Macqueen et al. 2017; Samy et al. 2017) have spurred investigation into the genome-wide differences among sympatric morphs.

Understanding the mechanisms responsible for the evolution of sympatric morphs is critical to the management and the conservation of their diversity. It is also necessary for the preservation of the unique ecological (e.g., piscivorous and planktivorous Arctic Charr, *Salvelinus alpinus*; Guðbrandsson et al. 2019) and economic (e.g., distinct fisheries for spring and fall-run Chinook Salmon, *Oncorhynchus tshawytscha*; Waples et al. 2004) roles served by sympatric salmonid morphs.

Here, we review the literature assessing the genetic differences among sympatric morphs within Salmonidae. We were particularly interested in investigating the ecological and genomic causes and consequences of sympatric salmonid morphs which demonstrate neutral and/or genome-wide genetic differentiation consistent with reproductive isolation and incipient speciation. Papers were found by querying Google Scholar for key terms such as “salmonid”, “sympatry”, “genetics” and salmonid species scientific names. Additional papers were sourced from the reference section of selected papers. Papers were selected if they studied the genetic differences among two or more sympatric morphs (meaning morphs “within cruising distance”; Mayr 1963) of a Salmonidae species using nuclear and/or mitochondrial markers. Our goal was to assess the contemporary genetic differences among sympatric salmonid morphs, the historical evolutionary processes that may have contributed to these differences, and the factors potentially influencing these genetic differences in the future. Specifically, we address the following questions: 1) What sympatric morph types exist in Salmonidae? 2) When

and how did the genetic differentiation between sympatric morphs arise? 3) Are genetic differences between sympatric morphs parallel within or among species? 4) Has historical allopatry and secondary contact influenced contemporary sympatric morph divergence? 5) What factors could change the genetic relationships among sympatric morphs in the future?

7.3 What sympatric morphs show evidence of incipient speciation within each genus of Salmonidae?

Genetically differentiated sympatric morphs are found across 5 genera (*Coregonus, Oncorhynchus, Prosopium, Salmo, Salvelinus*) and in populations across Asia, Europe, and North America. Below, we discuss the types of sympatric morphs found within each genus which demonstrate a level of neutral or genome-wide genetic differentiation consistent with incipient speciation. The defining characteristics of morphs varied widely within and among species but they generally fell within the same four categories found by Hudson et al. (2007) in their review of sympatric coregonid morphs including differences in: 1) migratory life history (including resident vs. anadromous and fluvial vs. adfluvial), 2) spawning location, 3) timing of spawning or run time, 4) trophic level or morphology. A fifth category, not included in Hudson et al. (2007), is cryptic differences, where genetic differentiation but not morphological or ecological differentiation was observed among morphs. Many sympatric morphs fit into multiple categories (e.g., both morphological and spawning location differences between morphs) and multiple types of sympatric morphs were observed in most species (Table 7.1). Below we describe the evidence by genus.

7.3.1 *Coregonus*

The occurrence of sympatric morphs within this group has been previously extensively reviewed by Hudson et al. (2007), but subsequent studies have come to light since. Sympatric morphs differing in spawning time occur in lacustrine *C. albula* (Delling et al. 2014) and *C. lavaretus* (Doenz et al. 2018) and anadromous *C. lavaretus lavaretus* (Vuorinen et al. 1981; Säisä et al. 2008). Most sympatric morphs differ morphologically and/or by trophic level. Sympatric lacustrine morphs differing in feeding habitat (either

the water column (limnetic morph) or the lake bottom (benthic morph)) are found in both *C. clupeaformis* and *C. lavaretus* (Jeukens et al. 2009). An additional profundal form found at the bottom of very deep lakes is sometimes observed in *C. lavaretus* (Præbel et al. 2013; Siwertsson et al. 2013). Benthic and profundal morphs are associated with low gill raker counts (which minimizes gill damage when suction feeding and forcing benthic debris through the gills) whereas limnetic morphs are associated with high gill raker counts (aiding entrapment of zooplankton via filter-feeding through the gills) (Willacker et al. 2010; Siwertsson et al. 2013). Limnetic and benthic *C. clupeaformis* morphs are small and large, respectively (Bernatchez et al. 1999) but small benthic morphs and large limnetic morphs are observed in some *C. lavaretus* populations (Huuskonen et al. 2017). Species flocks of up to six genetically distinguishable *C. lavaretus* morphs in European lakes are differentiated by a combination of morphology/trophic level, spawning time, and spawning location (Doenz et al. 2018). Sympatric lacustrine morphs of *C. artedi* may differ by size, gill raker count, and habitat depth (Turgeon et al. 1999; Turgeon and Bernatchez 2003; Ackiss et al. 2019). Sympatric morphs of *C. clupeaformis* with high and low gill raker counts may also differ in spawning times or locations (Bernatchez et al. 1996).

7.3.2 *Prosopium*

Despite being perceived as less prone to radiation than other salmonids, slight genetic differences based on allozymes have been detected between a sympatric large generalist morph and small zooplantivorous morph in Bear Lake, Utah (Vuorinen et al. 1998). In addition, three genetically differentiated morphs of *Prosopium* (differing in raker number and habitat depth) have been detected within Chignik Lake, Alaska (Gowell et al. 2012). Further investigation of morph differentiation in this genus is therefore warranted.

7.3.3 *Oncorhyncus*

Genetically distinguishable resident and anadromous morphs are observed within both *O. mykiss* (called Rainbow Trout and Steelhead Trout, respectively) and *O. nerka* (called Kokanee Salmon and Sockeye Salmon, respectively) (e.g., Foote et al. 1989;

Winans et al. 1996; Heath et al. 2008). Adfluvial and fluvial morphs of *O. mykiss* are also found in Lake Illiamna (Arostegui et al. 2019).

Sympatric morphs which differ in spawning or run time are observed within anadromous *O. gorbuscha* (Pink Salmon), *O. mykiss*, *O. nerka*, and *O. tshawytsha*. Anadromous *O. nerka* populations in the Yukon (Canada) and Russia have genetically differentiated early (June – August) and late run (August – December) morphs (Varnavskaya et al. 1994; Fillatre et al. 2003). Sympatric spring-run and fall-run anadromous morphs are observed in both *O. mykiss* and *O. tshawytsha* (Prince et al. 2017). An extreme example of spawning time differences is observed in *O. gorbuscha* where morphs spawn on alternative years (Limborg et al. 2014; Seeb et al. 2014).

Morphs can also differ by spawning location. For example, both resident and anadromous *O. nerka* may spawn in streams or on mainland beaches or island beaches within lakes (Taylor et al. 1997; Gomez-Uchida et al. 2011; Veale and Russello 2017b). Similarly, resident *O. mykiss* morphs spawned in different tributaries of Babine lake (Wellband and Heath 2013).

7.3.4 *Salmo*

Resident and anadromous forms are observed within both *S. salar* (Atlantic Salmon) and *S. trutta* (Brown Trout) (Verspoor and Cole 1989; Birt et al. 1991; Hindar et al. 1991; Giger et al. 2006). Adfluvial and fluvial Brown Trout populations can also occur in common watersheds (Giger et al. 2006). Genetically distinguishable adfluvial Atlantic Salmon populations are known to spawn in different rivers surrounding a common lake (Tessier et al. 1997). Genetic differences have also been detected between anadromous Atlantic Salmon differing in when they return to fresh water during their return migration (early in the season vs. late in the season) (O'Malley et al. 2014). Up to four morphologically differentiated forms of *S. trutta* are observed in large lakes within the British Isles. Examples of these morphs include a large piscivore (ferox), planktivore (sonaghen), benthivore (gillaroo), and a profundal form (Verspoor et al. 2019), which can also differ in spawning location within lakes (Ferguson and Taggart 1991). Sonaghen and ferox morphs may also have slight differences in spawning windows during the fall (Duguid et al. 2006). Genetically differentiated small *S. fibreni* and large *S. macrostigma*

spawn in different areas of a small karstic lake in Italy (Lake Posta Fibreno) (Gratton et al. 2013). Genetically distinguishable *S. ohridanus* and *S. trutta* co-occur in Lake Ohrid, Macedonia and differ by a variety of morphological traits (e.g., snout length, eye diameter, head shape, jaw length, number of dorsal and pectoral rays, number of gill rakers, and number of vertebrae and pyloric caeca) (Sušnik et al. 2006). However, given the estimated time of divergence between *S. ohridanus* and *S. trutta* of ~ 4 million years ago (Sušnik et al. 2006), these morphs could be considered different salmonid species rather than incipient sympatric morphs. Cryptic genetic differentiation that is unassociated with morphological differentiation is observed within some Swedish lacustrine populations of Brown Trout (e.g., Allendorf et al. 1976; Ryman et al. 1979; Palmé et al. 2013; Andersson et al. 2017a, 2017b).

7.3.5 *Salvelinus*

Several reviews have previously excellently outlined the breadth of sympatric morph types apparent in Lake Trout (*S. namaycush*) (Muir et al. 2016) and Arctic Charr (e.g., Jonsson and Jonsson 2001; Klemetsen 2013; Markevich and Esin 2018). Here we focus only on those sympatric morphs demonstrating genetic evidence of incipient speciation. Arctic Charr (Salisbury et al. 2018) and Brook Trout (*S. fontinalis*) (Jones et al. 1997) both demonstrate sympatric resident and anadromous forms. Adfluvial, large-bodied "Coasters" and fluvial, small-bodied resident Brook Trout occur in sympatry in Lake Superior (Burnham-Curtis 2001; D'Amelio and Wilson 2008; Scribner et al. 2012; Elias et al. 2018).

Fall-spawning and spring-spawning forms of lacustrine Arctic Charr are found in Fjellfrosvatn, Norway (Westgaard et al. 2004; Præbel et al. 2016) and Windermere Lake, England (Child 1984; Corrigan et al. 2011). Fall spawners in Windermere Lake spawn at shallower depths than spring spawners (Corrigan et al. 2011). Similarly, Brook Trout morphs in Mistassini Lake, Quebec, Canada are differentiated by whether they spawn in the lake's inflow or outflow (Fraser et al. 2004; Fraser and Bernatchez 2005).

The majority of sympatric *Salvelinus* morphs differ morphologically or by trophic level. Arctic Charr frequently differs by size into one of three size classes: dwarf, small, normal (Gordeeva et al. 2010, 2015). These size differences are often associated with

trophic level differences, for instance piscivores are typically larger than profundal forms which are usually dwarfs (Gomez-Uchida et al. 2008; Gordeeva et al. 2015; Doenz et al. 2019). Populations of Arctic Charr can contain various combinations of piscivores, planktivores, benthivores, and profundal forms (Magnusson and Ferguson 1987; Jacobs et al. 2020; Doenz et al. 2019). But as observed in *Coregonus*, where sympatric morphs occur in Arctic Charr, typically at least one exploits the benthic zone while another exploits the littoral zone. Multiple morphologically distinct morphs can occur in sympatry in both Arctic Charr and Lake Trout such as the piscivorous, small benthic, large benthic, and planktivorous Arctic Charr morphs in Thingvallavatn and the lean, humper, siscowet, and redfin Lake Trout morphs in Lake Superior (Dehring et al. 1981; Krueger et al. 1989; Page et al. 2004; Guinand et al. 2012; Baillie et al. 2016a, 2016b, 2018; Bernatchez et al. 2016; Perreault-Payette et al. 2017). Alternatively, Lake Trout, Arctic Charr and Dolly Varden (*S. malma*) also demonstrate cryptic genetic differences without associated morphological divergence (e.g., Wilson et al. 2004; May-Mcnally et al. 2015a; Marin et al. 2016).

7.4 When and how did the genetic differentiation between sympatric morphs arise?

7.4.1 Recent, polygenic origin of morphs

Consistent with incipient speciation, sympatric morphs can demonstrate very high genome-wide F_{ST} (e.g., Ackiss et al. 2020; Salisbury et al. 2020) as well as postzygotic barriers to gene flow (Fig.7.1). Such hybrid incompatibilities between dwarf (limnetic) and normal (benthic) *C. clupeaformis* were suggested by the increased gene expression variation in backcrosses (Dion-Côté et al. 2014), the varying numbers of chromosomes in the F1 (Dion-Côté et al. 2015) and intrachromosomal (heterochromatin and repeat region) variation between morphs (Dion-Côté et al. 2017). Reduced gene expression in hybrids of anadromous and resident Brook Trout similarly indicate hybrid incompatibilities (Mavarez et al. 2009). However, such strong genetic differences have likely accumulated only recently. Morphs generally do not differ by mtDNA, sharing either identical (e.g., Fraser and Bernatchez 2005) or nearly identical (e.g., Danzmann et al. 1991; Chouinard et al. 1996; Volpe and Ferguson 1996) haplotypes, supporting the recent evolution of morphs. Sympatric morphs may also share a common set of diverged haplotypes (e.g.,

the occurrence of Atlantic and Acadian lineage haplotypes in both sympatric dwarf and normal *C. clupeaformis* (Pigeon et al. 1997) and Atlantic and Arctic lineage haplotypes in both resident and anadromous *S. alpinus* (Salisbury et al. 2018)), suggesting that these morphs evolved following the introgression of these glacial lineages. Studies using nDNA also generally find that morph types occurring in sympatry are more genetically similar to each other than to allopatric populations of the same morph type (Table 7.2). Exceptions to this pattern are typically limited in geographic range (for examples, see supplementary information Appendix I). These results suggest a polyphyletic origin of sympatric morphs and that their genetic accumulated recently and within their local geographic areas. A similar recent, polygenic origin of sympatric morphs is also observed in non-salmonid species including *Osmerus mordax* (Taylor and Bentzen 1993a, 1993b) and *Gastrosteus aculeatus* (Taylor and McPhail 1999; Rundle et al. 2000).

7.4.2 Morphs fall along a continuum of speciation

Not all phenotypic differences occurring in sympatry within salmonids are necessarily associated with incipient speciation, however. Only a small degree genetic differentiation was observed between adfluvial, "coaster" and fluvial, resident Brook Trout in Lake Superior (Burnham-Curtis 2001; D'Amelio and Wilson 2008; Scribner et al. 2012; Elias et al. 2018). Similarly, planktivorous and piscivorous Kokanee Salmon in Jo-jo lake, Alaska were found to be genetically indistinguishable using both microsatellites (Shedd et al. 2015) and RAD-seq (Limborg et al. 2018). Sympatric littoral and pelagic morphs of Brook Trout demonstrated an insignificant pairwise F_{ST} based on five microsatellites (Dynes et al. 1999) despite support for a genetic component to these trophic differences based on reciprocal transplant experiments (Proulx and Magnan 2004). The absence of genetic differences among these sympatric morphs could be due to insufficient genomic coverage. However, sometimes variation in the magnitude of genetic differentiation between sympatric morphs is observed within a single study using a common marker set. For example, pelagic and benthic morphs of *C. lavaretus* had significant genetic differences in all but one of nine lakes in Norway (Østbye et al. 2006). Similarly, significant genetic differences were observed among beach and stream spawning Kokanee Salmon in only three of five lakes in British Columbia (Frazer and

Russello 2013). Genetic differences among morphs can also vary along a temporal dimension. Early and late run Sockeye Salmon (anadromous *O. nerka*) were genetically differentiated in all but one of six years of sampling of the Klukshu River, Yukon, Canada (Fillatre et al. 2003). Similarly, resident, and anadromous Brook Trout (*Salvelinus fontinalis*) were genetically distinguishable in one sampling year but not another in the Sainte-Marguerite River, Quebec, Canada (Thériault et al. 2007). These discrepancies in genetic differentiation may reflect variation in the selective pressures driving genetic divergence over space and time (Schluter and Nagel 1995) such that these populations may be at an earlier stage along a speciation continuum (Nosil et al. 2009) when morph differences are anticipated to be mostly plastic (Skúlason et al. 1999) (Fig.7.1).

Even if phenotypic differences among morphs have a genetic component, the further accumulation of genetic differences along this continuum is not inevitable. Such is the case for genes contributing to the "portfolio effect", generating diversity in life histories allowing populations to persist despite environmental fluctuations (Schindler et al. 2010, 2015; Jorde et al. 2018). These genes may be subject to balancing selection and will therefore be unlikely to drive genome-wide divergence and reproductive isolation among morphs (Micheletti et al. 2018). For example, red and white morphs in Chinook Salmon are the result of allelic variation within a single gene *BCO2-l* (Lehnert et al. 2016, 2019b). Maintenance of both morph types in sympatry is thought to be the result of balancing selection. Similarly, balancing selection maintains allelic variation in both the *greb1L* gene, which is responsible differences in run time in anadromous *O. tshawytscha* and *O. mykiss* (Hess et al. 2016; Prince et al. 2017; Micheletti et al. 2018; Narum et al. 2018; Thompson et al. 2019) and the *vgll3* gene, which is responsible for differences in sea age at maturity in Atlantic Salmon (Barson et al. 2015).

Given the right environmental context, however, allelic variation resulting in phenotypic differences could facilitate further genetic differentiation and eventually incipient speciation (Skúlason et al. 1999). An example of this is found in *O. mykiss* where a large, old double chromosomal rearrangement has been suggested as the source of divergence in life history of freshwater resident Rainbow and anadromous Steelhead Trout (Pearse et al. 2014, 2019). It has also been proposed that this inversion on Omy05

has been co-opted in Lake Iliamna, Alaska to differentiate fluvial and adfluvial Rainbow Trout (Arostegui et al. 2019). Genome-wide outliers outside of the Omy05 inversion have, however, been observed in distinguishing Rainbow from Steelhead Trout (Hecht et al. 2012, 2013; Hale et al. 2013) and fluvial from adfluvial Rainbow Trout (Arostegui et al. 2019). In addition, significant neutral genetic differences have been observed between Rainbow and Steelhead Trout (Heath et al. 2008). This suggests that incipient speciation between anadromous and resident and between fluvial and adfluvial morphs of *O. mykiss* have potentially been driven by this inversion. Inversions could play an important role in repeated sympatric morph differentiation as they provide a ready source of "pre-packaged" genomic variation (Wellenreuther and Bernatchez 2018). However, the importance of chromosomal inversions to sympatric morph differentiation in salmonids is generally unknown and requires further investigation. Also necessary is the identification of the contexts in which such standing variation can drive the further accumulation of morphological differentiation and reproductive isolation between sympatric morphs (Fig.7.1).

7.4.3 Potential drivers of incipient speciation of morphs

Environments with few other competing species and multiple open niche spaces, such as those post-glacial environments inhabited by many salmonids, are expected to favour genetic differentiation among morphs (Schluter et al. 1996b). The stable persistence of such environments can facilitate ecological speciation (where the occupation of distinct niche spaces leads to divergent selection) (Skúlason et al. 1999) and has likely played a major role in the evolution of sympatric morphs in postglacial fishes (Schluter 1996b; Smith and Skúlason 1996; Robinson and Parsons 2002; Snorrason and Skúlason 2012). In support of this idea is the observation that genetic and phenotypic differentiation are correlated between sympatric morphs of *S. alpinus* (Gíslason et al. 1999; Corrigan et al. 2011). Sympatric morphs of *S. alpinus* are also more commonly observed in larger, deeper lakes, with few species (Griffiths 1994; Riget et al. 2000), suggesting that niche availability prompts morph differentiation. In addition, the observation that highly genetically differentiated regions of the genome were associated with both expression (eQTL) and phenotypic (QTL) differences among dwarf and normal

C. clupeaformis (expression QTL) support the ecological speciation of these morphs (Whiteley et al. 2008; Renaut et al. 2011, 2012). Alternatively, increased intraspecific competition within and among morphs due to reduced niche space could also lead to stronger divergent selection between morphs (Landry et al. 2007). For example, greater phenotypic and genetic differentiation of dwarf and normal *C. clupeaformis* were observed in lakes with reduced oxygen in the hypolimnion (Landry et al. 2007). Sexual selection may also play an important but underappreciated role in the formation of sympatric salmonid morphs. Although salmonids demonstrate mate choice based on factors including body size, colour, dominance, and even MHC similarity, there has been little investigation of how such mate choice might facilitate incipient speciation (Auld et al. 2019). Isolation by time (Hendry and Day 2005) could also reduce gene flow and increase genetic differentiation in those sympatric morphs with differences in spawning time. Similarly, the strong philopatry in most salmonid species could cause reproductive isolation on a very small scale (Hendry et al. 2004), even within lakes as is observed in mainland and island spawning *O. nerka* (Gomez-Uchida et al. 2011). In addition to these factors, all of which could all operate in sympatry, recent and local allopatry could also rapidly increase reproductive isolation among morphs (Rice and Hostert 1993).

During their postglacial recolonization, many salmonid populations became trapped in fresh water due to isostatic rebound (Power 2002a; Klemetsen et al. 2003) leading to the rapid genetic differentiation of these isolated landlocked populations by way of genetic drift and adaptation (Bell and Andrews 1997; McDowall 2001; Salisbury et al. 2016, 2018, 2020; Delgado et al. 2020). This genetic differentiation could be maintained if such populations subsequently regain connectivity and admix with other populations resulting in the occurrence of sympatric genetically distinguishable morphs descended from each of the admixed populations. Supporting this hypothesis is the observation that genetic differences among resident and anadromous Atlantic Salmon populations were higher when they had historically been separated by dams than when they had always occurred in sympatry (Adams et al. 2016). Additionally, cryptic morphs of Brown Trout (Allendorf et al. 1976; Ryman et al. 1979; Andersson et al. 2017a, 2017b) have been observed in paired landlocked lakes connected by a short waterway. In these cases, two genetic subgroups are observed, but each occur in both lakes. We

speculate that these genetic subgroups could be the result of mixing of previously isolated lake populations. Alternatively, cryptic genetic differentiation could be the result of multiple colonization events (Andersson et al. 2017a). The importance of such "microallopatry" events (Johannesson 2001) to morph divergence can be difficult to study without knowledge of the barriers to gene flow on a fine geographic scale since the time of colonization. For example, Kapralova et al. (2011) and Jacobs et al. (2020) could not distinguish whether recent allopatry or sympatry best explained the genetic differentiation among contemporarily sympatric Arctic Charr morphs. Genetic information may therefore be insufficient to identify the factors driving sympatric morph differentiation and interdisciplinary comparisons of ecological, behavioural, and geological studies with genetic data are therefore needed to tease apart the potential causes of incipient speciation.

7.5 Are genetic differences between sympatric morphs parallel within or among species?

Although the drivers of morph differentiation may not always be known, the recent evolution of most sympatric morphs make them a useful model to investigate the repeatability of speciation (Elmer and Meyer 2011) and the relative influence of contingency and determinism (Blount et al. 2018). A lack of genetic parallelism of sympatric morphs across locations would suggest the availability of multiple genetic pathways to achieve similar phenotypic differentiation and reproductive isolation (Elmer and Meyer 2011). In such cases, morph differentiation may be limited by a lack of driving environmental processes (e.g., selection) (Rundle and Nosil 2005). Alternatively, morph differentiation which is consistently driven by a specific locus is more likely to be limited by a lack of genetic capacity (i.e., an absence of genetic variation at the locus driving morph differentiation) (Elmer and Meyer 2011). The degree of parallelism exhibited by sympatric morphs will therefore inform whether their conservation should be predicated upon the maintenance of habitat or the specific genetic variation known to deterministically drive speciation.

7.5.1 Magnitude of genomic parallelism

Direct comparisons of the magnitude of genomic parallelism across studies and species is complicated by the fact that the null model of expected parallelism is difficult to quantify and is also dependent on factors such as demographic history that may vary between systems (Lee and Coop 2019). Despite this caveat, it is notable that limited genetic parallelism is commonly observed among sympatric salmonid morphs across locations. Across 11 studies (Table 7.3), of those markers identified as outliers, only an average of 11% were detected in more than one population. Similarly, the double inversion of Omy05 that has been inferred to dictate migratory life history in *O. mykiss* was found to not be diagnostic of this trait in populations from South Fork Eel River, California (Kelson et al. 2019) and Alaska (Weinstein et al. 2019). Only 45% of the variation in life history was explained by the combined effects of sex and this inversion genotype, suggesting other plastic or genetic factors could be influential in dictating this trait (Kelson et al. 2019). A lack of parallelism could reflect a mosaic of selective pressures across locations. Larson et al. (2019) found that 7 SNPs in islands of genomic divergence in three linkage groups were repeatedly detected as outliers across 32 populations of *O. nerka*, but not consistently across all drainages. Similarly, Dion-Côté et al. (2017) found intrachromosomal differences potentially contributing to reproductive isolation between sympatric benthic and limnetic *C. clupeaformis* were non-parallel across locations. These results suggest that the genetic differentiation of morphs is often population-specific and the genes driving morph differentiation, even those demonstrating parallelism on a local scale, may not be employed across the entire range of a species. Low degrees of parallelism within species could also be due to low sequencing coverage missing the actual genes under selection. Alternatively, non-adaptive processes contributing to genomic patterns of differentiation among morphs (e.g., drift, mutation rate differences, hitchhiking, and meiotic drive) (Wolf and Ellegren 2017) could swamp parallel signals of selection. However, genes which do demonstrate parallelism could be responsible for consistently driving morph divergence across locations and their discovery is critical for the conservation of sympatric morphs.

7.5.2 Genes demonstrating parallelism within and among species

The parallel evolution of morphs is however, supported by the independent identification of outlier loci by multiple studies among sympatric morphs of the same species. Both Heath et al (2008) and Hale et al. (2013) found that gonadotropin II subunit β significantly differentiated some Rainbow Trout and Steelhead Trout populations. One outlier SNP differentiating Kokanee Salmon and Sockeye Salmon in Redfish lake, Idaho, USA (Nichols et al. 2016) corresponded to the gene *DVR1* (decapentaplegic and Vg-related 1), identified as a gene which also significantly differentiates beach and stream spawning Kokanee Salmon in Okanagan Lake, British Columbia, Canada (Lemay and Russello 2015). Eighteen outlier regions detected among *O. nerka* morphs by Veale and Russello (2017b) differentiated sympatric morphs of *O. nerka* in Nichols et al. (2016) and Larson et al. (2017). *Lrrc9* significantly differentiated beach-spawning and stream-spawning fish (of both Sockeye and Kokanee Salmon) (Nichols et al. 2016; Veale and Russello 2017b; Larson et al. 2017, 2019). This gene demonstrated 181 fixed differences among shore and stream spawning *O. nerka* and diverged about 3.8 mya (Veale and Russello 2017a). Salmonids may therefore consistently reuse old standing genetic variation to rapidly drive contemporary sympatric divergence as has been observed in other radiating clades such as cichlids (Meier et al. 2017).

Parallelism is further supported by the observation of the same loci showing genetic differentiation among sympatric morphs in multiple species. Major Histocompatibility Complex (MHC) I and II were found to differentiate sympatric morphs in a number of species including *C. lavaretus* (Feulner and Seehausen 2019), *O. mykiss* (Hale et al. 2013), *O. nerka* (Gomez-Uchida et al. 2011, McGlauflin et al. 2011, Larson et al. 2014), and Arctic Charr (Conejeros et al. 2014). However, the MHC may be influenced by factors other than morph type since differentiation within MHC II was found to correlate more with depth than with Lake Trout morph in Lake Superior (Baillie et al. 2018). In addition, MHCII was not important in differentiating Rainbow from Steelhead Trout (Heath et al. 2008). Non-parallel differences at the MHCIIβ locus between replicate pairs of benthic and limnetic *C. clupeaformis* suggests that this gene does not drive phenotypic differences between morphs (Pavey et al. 2013). However, our review of the literature identified a number of other genes which differentiate sympatric

morphs in multiple salmonid species (Table 7.4). The repeated detection of a minority of genes as important for morph differentiation both within and among species therefore supports the potential for genetic parallelism (Schluter and Nagel 1995).

7.5.3 Parallelism at multiple levels

While most investigation has focused on consistent differences in alleles or genes, other levels of parallelism may also contribute to consistent sympatric morph differentiation in salmonids (Fig.7.2). This potential for parallelism at other levels may help to explain the generally low degree of parallelism observed at the level of the allele and gene in salmonids (Jacobs et al. 2020).

Genetic parallelism at the level of the paralog has been largely unstudied despite its potentially significance for morph differentiation in salmonids. The whole genome duplication (WGD) at the base of the salmonid clade between 88 – 102 mya (Macqueen and Johnston 2014) allows for the possibility of the employment of homeologous copies of the same gene to drive morph differentiation (Nichols et al. 2008). QTL associated with morphological differences among Steelhead and Rainbow Trout have been found on homeologous chromosomes, suggesting that homeologs may each retain or collaboratively contribute to a common functionality (Nichols et al. 2008). Intriguingly, genes detected in the double chromosomal inversion on Omy05 (Pearse et al. 2019) contained homeologs of the CLOCK gene in Omy01 and of the MAPK10 gene in Omy12 each of which had previously been identified as significantly differentiating Rainbow and Steelhead Trout (Nichols et al. 2008; Hecht et al. 2013). This suggests the potential for the employment of different homeologous copies to achieve similar phenotypic divergence among morphs (Pearse et al. 2019). Salisbury et al. (2020) also found several instances where different paralogous copies of the same gene were detected as outliers between sympatric, size-differentiated Arctic Charr morphs across three locations. However, despite the potential importance of the WGD, its influence on sympatric speciation in salmonids remains relatively unexplored and requires further study (Nichols et al. 2008).

The level of parallelism contributing to sympatric morph differentiation may not always be genetic, however. A growing body of research suggests that gene expression

differences can play a critical role in differentiating sympatric morphs (e.g., Bernatchez et al. 2010). Such consistent expression differences between similar morph types may even be apparent across species. For example, trypsin and carboxylesterase demonstrated parallel gene expression differences between dwarf and normal morphs of *C. clupeaformis* with ecologically similar limnetic and benthic morphs of *C. lavaretus* (Jeukens et al. 2009). Among dwarf and normal *C. clupeaformis*, 18% (51 of 278) and 24% (248 of 1047) of differentially expressed genes in white muscle and liver (respectively) were detected in more than one location (Derome et al. 2006; St-Cyr et al. 2008). In comparison, only 6 of 48 (13%) outlier AFLPs were detected in more than one location containing dwarf and normal *C. clupeaformis* (Campbell and Bernatchez 2004). A few key regulator genes might therefore drive the greater consistency in transcriptomic rather than genomic differences across replicate sympatric morphs (Bernatchez et al. 2010). This is supported by the identification of a handful of genomic regions ("eQTL hotspots") associated with the differential expression of multiple ofther genes in the brain (Whiteley et al. 2008) and muscle (Derome et al. 2008) between *C. clupeaformis* morphs. Furthermore, consistent gene expression differences in pyruvate kinase between limnetic and benthic morphs in both *C. lavaretus* and *C. clupeaformis* were found to be associated with a common SNP in the 3'UTR of this gene for both species (Rougeux et al. 2019b). Alternatively, Jacobs et al. (2020) observed consistent expression differences between sympatric Arctic Charr morphs across Scottish and Transbaikalian locations that did not have a common genetic driver. These results suggest that parallel expression differences, potentially without a common genetic basis, may facilitate consistent phenotypic differentiation among sympatric morphs.

Multiple levels of parallelism may contribute to morph differentiation, yet the relative importance of each level and the evolutionary context in which each level is most likely to be important, is currently unknown. Further study of the influence of other levels of parallelism to sympatric morph differentiation, beyond that of the gene or allele, are therefore warranted.

7.6 Has historical allopatry and secondary contact influenced contemporary sympatric morph divergence?

Although most sympatric salmonid morphs appear to have evolved recently, glacial origin as well as secondary contact of historically allopatric glacial lineages may have critically informed the genetic variation available to be divvied up among sympatric morphs. Almost all salmonid species exhibiting sympatric morphs were separated into multiple separate glacial refugia during the Pleistocene including in: *C. artedi* (2 lineages, Turgeon et al. 1999; Turgeon and Bernatchez 2003), *C. clupeaformis* (5 lineages, Bodaly et al. 1992; Bernatchez and Dodson 1994), *C. lavaretus* (3 lineages, Østbye et al. 2005a), Arctic Charr (5 lineages, Brunner et al. 2001; Moore et al. 2015), Brook Trout (6 lineages, Danzmann et al. 1998), Lake Trout (6 lineages, Wilson and Mandrak 2004), *O. nerka* (2 lineages, Taylor et al. 1996; Beacham et al. 2006b), *O. mykiss* (2 lineages, McCusker et al. 2000), *O. tshawytscha* (2 lineages, Beacham et al. 2006a), Brown Trout (5 lineages, Bernatchez 2001), Atlantic Salmon (2 lineages, Nilsson et al. 2001; Rougemont and Bernatchez 2018). In addition, sympatric morphs are frequently observed in coregonids in areas of secondary contact between multiple glacial lineages (Hudson et al. 2007). Examples include in the secondary contact zone between the Atlantic and Acadian glacial lineages of *C. clupeaformis* (Bodaly et al. 1992; Bernatchez et al. 1996; Pigeon et al. 1997), between the southern and northern European glacial lineages of *C. lavaretus* (Østbye et al. 2005a), and between Mississippian and Atlantic glacial lineages of *C. artedi* (Turgeon and Bernatchez 2001). Despite this, the relative influence of such secondary contact events on sympatric morph differentiation is generally uncharacterized, though it has been best studied in coregonids and Arctic Charr.

Some sympatric morphs could be due to distinct glacial lineages maintaining reproductive isolation upon secondary contact, with each glacial lineage occupying a unique niche towards which it was predisposed (Fig.7.3b). This is supported in dwarf and normal *C. clupeaformis* in Cliff Lake which are alternatively fixed for Acadian and Atlantic lineage mtDNA, respectively (Pigeon et al. 1997). However, sympatric pale and dark morph Arctic Charr in Gander Lake were initially thought to be founded separate glacial lineages due to their significant ecological, phenotypic, and genetic differences (Gomez-Uchida et al. 2008), this was later contradicted by the observance of Atlantic

haplotypes in both morphs (Salisbury et al. 2019). In addition, the occurrence of a single pale morph individual with an Acadian haplotype suggested that the Acadian and Atlantic lineages had introgressed prior to the divergence of these two morphs (Salisbury et al. 2019).

However, it is possible that introgression may occur between glacial lineages except for the genes responsible for phenotypic differences between sympatric morphs. In this case, a common set of "outlier alleles" from a single glacial lineage typifies each morph despite some introgression elsewhere in the genome (Fig.7.1c). Such a scenario may have occurred in sympatric benthic and limnetic morphs of *C. clupeaformis* and *C. lavaretus* in eastern North America and Europe, respectively. Sympatric morphs in both species are often found in secondary contact zones of multiple glacial lineages (Pigeon et al. 1997; Østbye et al. 2005a). Demographic modelling supports a scenario of secondary contact contributing to sympatric morph differentiation in both species suggesting that the genetic variation differing between sympatric morphs may be sourced from alternative glacial lineages in each morph (Rougeux et al. 2017, 2019a). Detecting such a scenario therefore requires accurate demographic modelling and knowledge of the genetic variation of each founding lineage.

Alternatively, some lineages may be more predisposed to radiation than others (Rabosky et al. 2007; Losos 2010; Wagner et al. 2012). This may be apparent over a large geographic scale if sympatric morphs are only apparent in populations descendant from a particular glacial lineage. All four morphs of Lake Trout in Great Bear Lake are of Mississippian origin, suggesting this lineage's propensity for divergence (Harris et al. 2015). Similarly, sympatric morphs have been observed in populations descended from single lineages of *C. clupeaformis* (Bernatchez et al. 1996; Pigeon et al. 1997) and *C. lavaretus* (Østbye et al. 2005a). "Hot spots" of sympatric Arctic Charr morphs have been found in Transbaikalia, Scotland, Scandinavia, and Iceland (Markevich and Esin 2018) all of which were founded by the Atlantic or Siberian glacial lineages (Brunner et al. 2001; Moore et al. 2015). These two lineages are sister clades (Brunner et al. 2001; Moore et al. 2015), therefore, the capacity for sympatric divergence among Arctic Charr may have evolved independently within each of these lineages or within the common ancestor of these lineages. In populations within the secondary contact zones of multiple

glacial lineages, if the sympatric morph differentiation is due to a single lineage predisposed to radiation, then the genes differentiating morphs should have allelic variation sourced from a common lineage in all morphs (Fig.7.3d).

The increased genetic diversity of hybrid swarms resulting from recent secondary contact events could allow for new combinations of adaptive loci (Seehausen 2004) and loci which are barriers to gene flow (Seehausen 2013). These could then become subject to divergent selection, driving incipient speciation (Abbott et al. 2013; Marques et al. 2019). Hudson et al. (2007)'s extensive review of sympatric divergence within *Coregonus* suggested that hybrid radiation after secondary contact was the most likely cause of divergence within most populations. The number of *C. lavaretus* morphs in European lakes often exceeds the number of glacial lineages that have contributed to a population, further supporting morph radiation as a consequence of ancient hybridization events (Hudson et al. 2007). Where sympatric morphs have arisen from hybrid swarms, we might expect a "combinatorial" signature of speciation (Marques et al. 2019), where the alleles differentiating sympatric morphs at outlier loci can come from any glacial lineage (Fig.7.3e).

These genomic consequences of secondary contact on contemporary morph differentiation are not mutually exclusive. The outlier alleles driving morph differentiation may vary in their glacial lineage origin by population or genomic region. It is currently unclear which of these potential modalities in which secondary contact of glacial lineages may influence incipient speciation is most likely, nor in what evolutionary contexts each is most likely to occur. Further investigation of the source of those alleles driving reproductive isolation and/or phenotypic differences between sympatric morphs is therefore needed and could be accomplished by whole genome comparisons of each sympatric morph to representative populations of each ancestral lineage. Given that interspecific hybridization between salmonid species is also known to occur (Verspoor and Hammar 1991), similar analyses could help to assess if this interspecific hybridization has also critically informed contemporary morph differentiation. Such research has important conservation implications because it will inform us not only of the origin of the genetic and phenotypic variation we are interested

in preserving but also the contemporary distribution of this genetic variation (Rundle and Nosil 2005).

7.7 What factors could change the genetic relationships among sympatric morphs in the future?

In addition to historical processes, an understanding of the contemporary factors influencing the genetic divergence among sympatric morphs is critical for their management into the future. However, the genetic differentiation among most sympatric morphs has arisen only recently (see section 7.4.1, above). This suggests genetic differences among morphs may be vulnerable to erosion, leading to the collapse of morphs into a single population (Hudson et al. 2011).

7.7.1 Erosion of morph differences due to niche perturbation

Genetic divergence among morphs is thought to be at least partially driven by environmentally driven divergent selection resulting in ecological speciation (Schluter 1996a, 1996b; Orr and Smith 1998). Correlations of the number and genetic differentiation among Arctic Charr morphs with lake size and depth (Gíslason et al. 1999; Gordeeva et al. 2015; Doenz et al. 2019), support the importance of niche availability to morph differentiation. Niche destruction could therefore diminish divergent selection pressure and erode genetic differences among morphs (Seehausen 2006). This was observed among *Coregonus* species in Swiss lakes where eutrophication in the 1950s was correlated with decreased F_{ST} values among morphs (Vonlanthen et al. 2012). Lakes with higher eutrophication values were also observed to have fewer outlier AFLPs among morphs, suggesting an erosion of genetic differences (Hudson et al. 2013). Profundal and benthic morphs may be particularly susceptible to eutrophication which deoxygenates lakes (Bittner et al. 2010; Feulner and Seehausen 2019). Alleles previously private to an extinct profundal species in Lake Constance (*C. gutturosus*) were observed in contemporary extant coregonid species, indicating that introgression may have caused the loss of this species (Vonlanthen et al. 2012). Similar reductions in genetic differences among benthic and limnetic *G. aculeatus* have been observed after environmental disturbances (Gow et al. 2006; Taylor et al. 2006). The introduction of non-native species

can also decrease morph genetic differentiation if the introduced species outcompetes one particular morph. After the introduction of *C. albula*, a superior zooplanktivore to the limnetic morph of *C. lavaretus,* an increase in hybrids between the benthic and limnetic morphs of *C. lavaretus* was observed in Lake Skrukkebukta, Norway (Bhat et al. 2014). Multiple stressors lead to the reduced genetic distinctiveness of Lake Superior Lake Trout morphs. Genetic differentiation among and allelic richness within lean, humpers, and siscowet morphs were reduced between 1948 – 1959 and 2004-2013 possibly as result of the stocking of hybrid ecotypes in the 1950s to 1980s, introduction of non-native rainbow smelt (*Osmerus mordax*), introduction of the parasitic sea lamprey, and the intense fishery in the 1900s (Guinand et al. 2012; Baillie et al. 2016b). The percentage of shared MHCIIβ alleles jumped from 20% to 35% between assessments done by Noakes et al. (2003) and Baillie et al. (2018) suggesting the collapse of genetic differences among morphs between studies (Baillie et al. 2018).

7.7.2 Erosion of morph differences due to increased gene flow

Stocking is an additional threat since it can enhance gene flow among morphs, swamping their genetic differentiation. Stocking may have contributed to the erosion of genetic differences among adfluvial populations of Atlantic Salmon in Lac St-Jean (Tessier and Bernatchez 1999). Hatchery-raised fish were genetically distinguishable from the river populations into which they were introduced (Tessier et al. 1997). The stocking of salmonid populations containing sympatric morphs is widespread (e.g., Narum et al. 2004; Säisä et al. 2008; Mehner et al. 2010; Smith and Engle 2011; Hudson et al. 2011, 2017; Vonlanthen et al. 2012; Eckmann 2015; Baillie et al. 2016b, 2018; Huuskonen et al. 2017; Doenz et al. 2018; Lemopoulos et al. 2018). Therefore, careful consideration of the genetic relationships among hatchery and wild morphs is required to prevent hatchery fish facilitating gene flow among wild sympatric morphs.

Given the potential for multiple anthropogenic stressors affecting sympatric salmonid morphs, a greater understanding of the relative and interactive effects of these stressors on sympatric morphs is critical for maintaining these polymorphisms. Since a majority of studies capture the genetic divergence of morphs at a single point in time it is difficult to discern whether genetic differences are accumulating or eroding and which

processes are influencing this change. Further study of the genetic differentiation among morphs over a temporal scale is therefore urgently needed.

7.8 Conclusions

In this review we attempted to address six major questions concerning genetic differentiation among sympatric salmonid morphs. Our findings are summarized as follows:

1. Sympatric salmonid morphs can be phenotypically differentiated by migratory life history, spawning location, spawning or run time, or trophic level or morphology. Alternatively, some genetically differentiated sympatric morphs may be cryptically phenotypically differentiated.
2. The majority of neutral and/or genome-wide genetic differentiation among morphs has arisen recently and locally. Potential sources of such genetic differentiation include: ecological speciation, sexual selection, reductions in gene flow due to differences in spawning times or locations, and secondary contact after microallopatry.
3. Phenotypic differences in sympatry are not always associated with incipient speciation and may be due to plasticity or standing variation. These populations may be at an earlier stage along the speciation continuum. Therefore, depending upon the environmental context standing variation in one population may drive incipient speciation in another.
4. For those sympatric morphs demonstrating significant genetic differences consistent with incipient speciation, this genetic differentiation is largely non-parallel across populations and species. However, a few key genes show potential for consistently driving incipient speciation.
5. Support for the hypotheses that 1) secondary contact of historically allopatric populations has fueled sympatric divergence and 2) some glacial lineages are more predisposed to sympatric divergence than others, is equivocal at this point. Further study of Arctic Charr and coregonid species will be useful since these species have multiple glacial lineages and secondary contact zones.

6. Although strong genetic differentiation is observed among some sympatric morphs, this genetic differentiation is vulnerable to erosion if selective pressures weaken or change. Niche destruction and inappropriate stocking practices can reverse speciation.

These findings suggest that genetic differences among sympatric morphs accumulated recently and are non-parallel across populations except for a few genes. The detection of genes demonstrating parallelism both within and among salmonid species suggests that morph differentiation may be genetically constrained (Elmer and Meyer 2011). It is possible that as with *lrrc9* (Veale and Russello 2017a), allelic variations of the genes demonstrating parallelism have existed as standing variation for a long period of time. Sticklebacks (Ishikawa et al. 2019), cichlids (Meier et al. 2017), and saltmarsh beetles (Van Belleghem et al. 2018) have all reused old standing variation to drive their morph divergence. Genes demonstrating parallelism are therefore excellent candidates as sources of "magic traits" that are acted upon by divergent selection while reducing gene flow (Servedio et al. 2011). Such genes could be responsible for the consistent phenotypic differences observed among repeated sympatric morphs and their discovery is critical for the conservation of sympatric morphs. However, their identification among reproductively isolated morphs may be hampered by drift swamping signals of selection (Nosil et al. 2009a). Processes other than selection can also contribute to genomic patterns of differentiation among morphs (e.g., mutation rate differences, hitchhiking, and meiotic drive) (Lynch 2007; Wolf and Ellegren 2017). The comparison of multiple consistently differentiated sympatric morphs, occurring across a large geographic area, with differing glacial histories, and with greater genomic coverage will aid in the detection and verification of putative speciation genes.

However, most of the genetic differentiation among morphs is generally non-parallel across locations. This suggests the importance of local adaptation to morph differentiation (Taylor 1991; Fraser et al. 2011). Quantification of the phenotypic parallelism demonstrated by sympatric morphs across locations could help to identify systems where local adaptation is important and temper our expectations of genetic parallelism (Oke et al. 2017). Alternatively, some of the consistent phenotypic divergence observed across populations might be achieved through non-parallel genetic pathways

(Elmer and Meyer 2011). This ambiguity could be resolved by taking a mechanistic approach (Dalziel et al. 2009). Investigating the developmental consequences of non-parallel outlier genes could distinguish those that dictate phenotypic divergence at a local scale versus those that dictate a phenotypic divergence observed more broadly across all replicate sympatric morphs. Additional comparisons of the developmental consequences of parallel versus non-parallel genes are needed to determine their relative contributions to reproductive isolation and adaptive phenotypic differentiation among morphs. Such studies will be essential to our understanding of the genomic consistency of speciation.

In addition to the developmental context, an understanding of the genomic consistency of speciation will require further consideration of the ecological and evolutionary contexts of morph differentiation (Govaert et al. 2019; Skúlason et al. 2019). In this review we found that the consistency of morph differentiation may be tempered by both historical evolutionary processes (e.g., glacial history) and contemporary ecological processes (e.g., gene flow, selection) much like both historical and contemporary processes can influence the genetic structure of non-equilibrium populations (e.g., Vera-Escalona et al. 2015; Salisbury et al. 2016; Ruzzante et al. 2019). Further investigation of the factors driving genomic differentiation will be essential to assess if the absence of genetically differentiated morphs is due to a lack of genetic capacity (due to glacial history, recent bottlenecks, contemporary high gene flow) or due to a lack of divergent selective pressure. Such an understanding will require research to compare the genetic structure, contemporary environmental differences, and demographic histories of populations both with and without sympatric morphs. This will allow greater insight into the ecological factors triggering divergent selection as well as the evolutionary origins of the allelic variation contributing to morph differentiation (Govaert et al. 2019; Skúlason et al. 2019).

Salmonidae are likely to continue to be an ideal model for studies of incipient speciation. Our review indicates that many salmonid species demonstrate multiple instances of consistent, yet evolutionarily independent morph differentiation. The many ways in which morphs can be differentiated within salmonids gives opportunities to study multiple types of incipient speciation. Additionally, the occurrence of similar types of differentiation (e.g., residency/anadromy) across multiple salmonid species allows for

testing the relative importance of determinism and contingency on speciation at a greater level of evolutionary independence than when making comparisons within a species (Elmer and Meyer 2011, Blount et al. 2018, for examples of interspecific comparisons see Derome and Bernatchez 2006, Jeukens et al. 2009). Comparisons at an even greater level of evolutionary independence could be made between sympatric morphs in Salmonidae and those in its sister clade, Galaxiidae (Rosen 1974, Johnson and Patterson 1996). Though comparatively understudied, galaxiids demonstrate much of the phenotypic variation which make salmonids such ideal models of speciation (Milano et al. 2002, 2006, Delgado et al. 2019, 2020). This phenotypic variation observed among salmonid sympatric morphs suggests that insights gained from studying speciation within Salmonidae are likely to be relevant beyond this clade. Future studies should capitalize on this family's growing genomic resources, as well as its conduciveness to laboratory studies (Skúlason et al. 2019). However, Salmonidae has a number of limitations as a model for studying incipient speciation. The large genome sizes characterizing salmonids (Hardie and Hebert 2004) result in more pronounced trade-offs between sample number, genomic coverage, and genomic depth. Long maturation times (>1 year) in salmonids (Scott and Crossman 1973) largely prevent intergenerational experimental studies. Finally, many wild populations of salmonids are highly influenced by human effects including stocking and transportation (Katz et al. 2013; Forseth et al. 2017), which can blur evolutionary signals (though introduced salmonid populations which subsequently evolve sympatric morph could make useful experimental systems e.g., the evolution of even-year spawning Pink Salmon from introduced odd-year spawners in the Great Lakes (Wen-Hwa and Lawrie 1981)). Therefore, despite these potential drawbacks, understanding of the sympatric polymorphisms present in salmonids is critical for their conservation in the face of these growing anthropogenic threats. Increased sequencing power and genomic references for this family are also likely to alleviate some of these potential issues. The value of Salmonidae as a model for uncovering the mysteries of the genomic mechanisms of speciation has therefore likely yet to be fully realized.

7.9 Figures

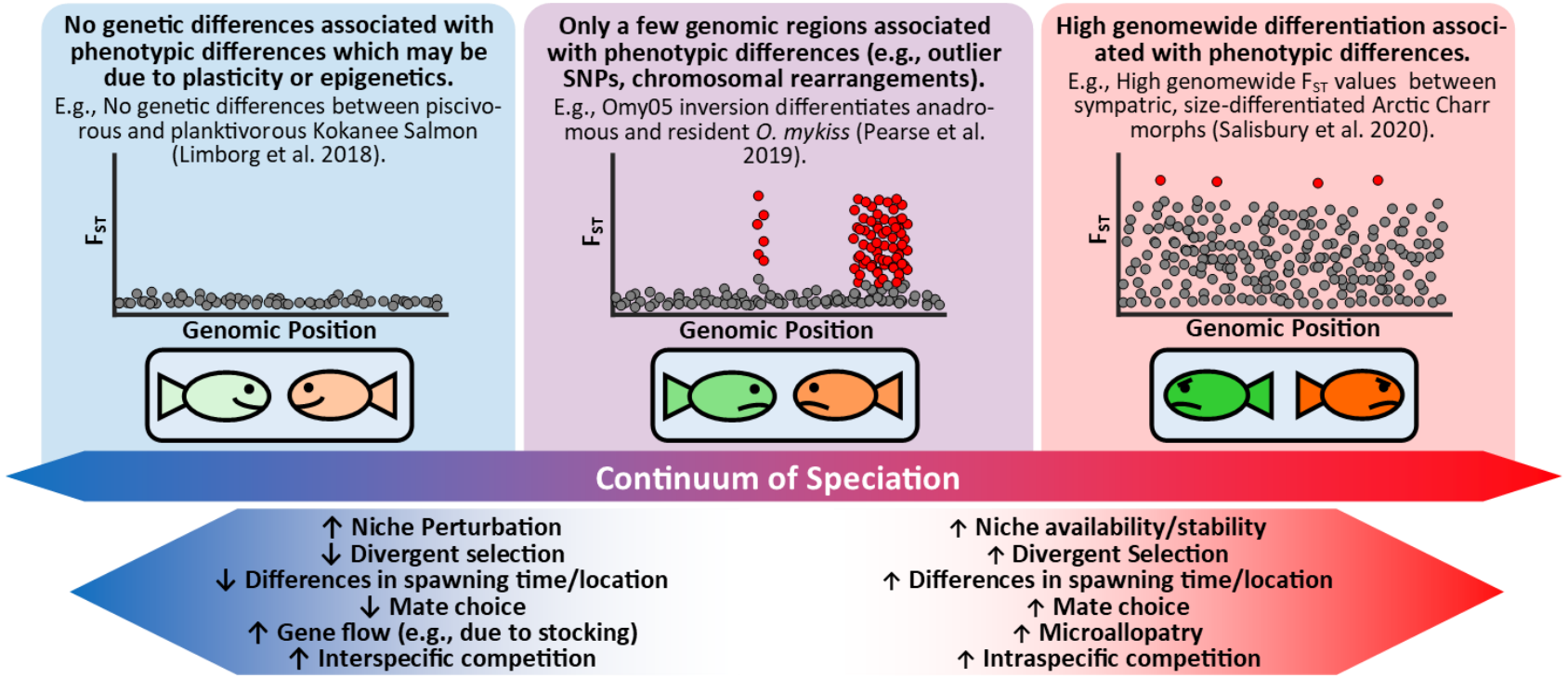

Fig.7.1 Continuum of genetic differentiation between sympatric morph and the factors which may drive (red arrow) or erode (blue arrow) such genetic differences.

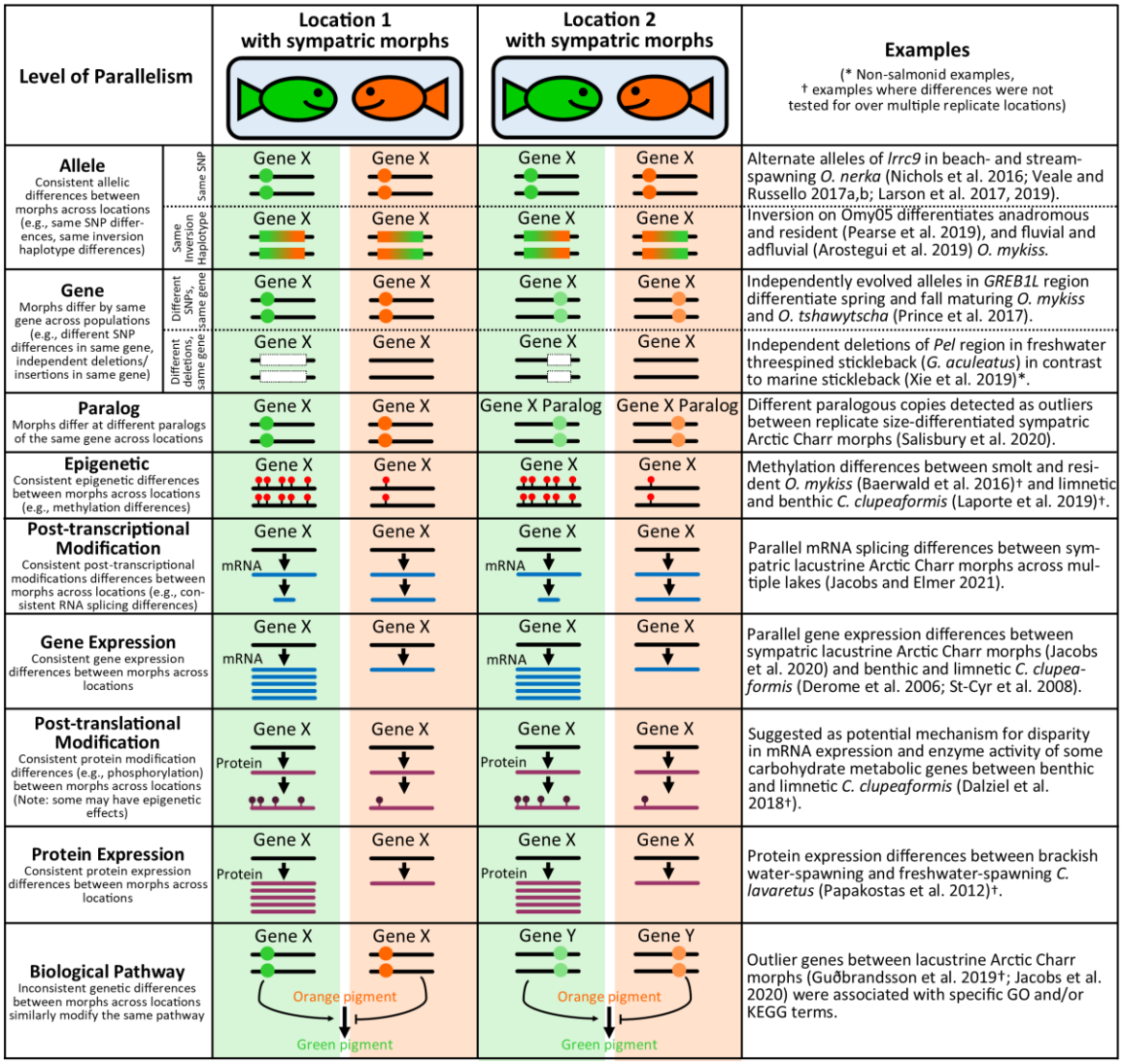

Fig.7.2 Levels of parallelism which could contribute to phenotypically consistent sympatric morph differentiation.

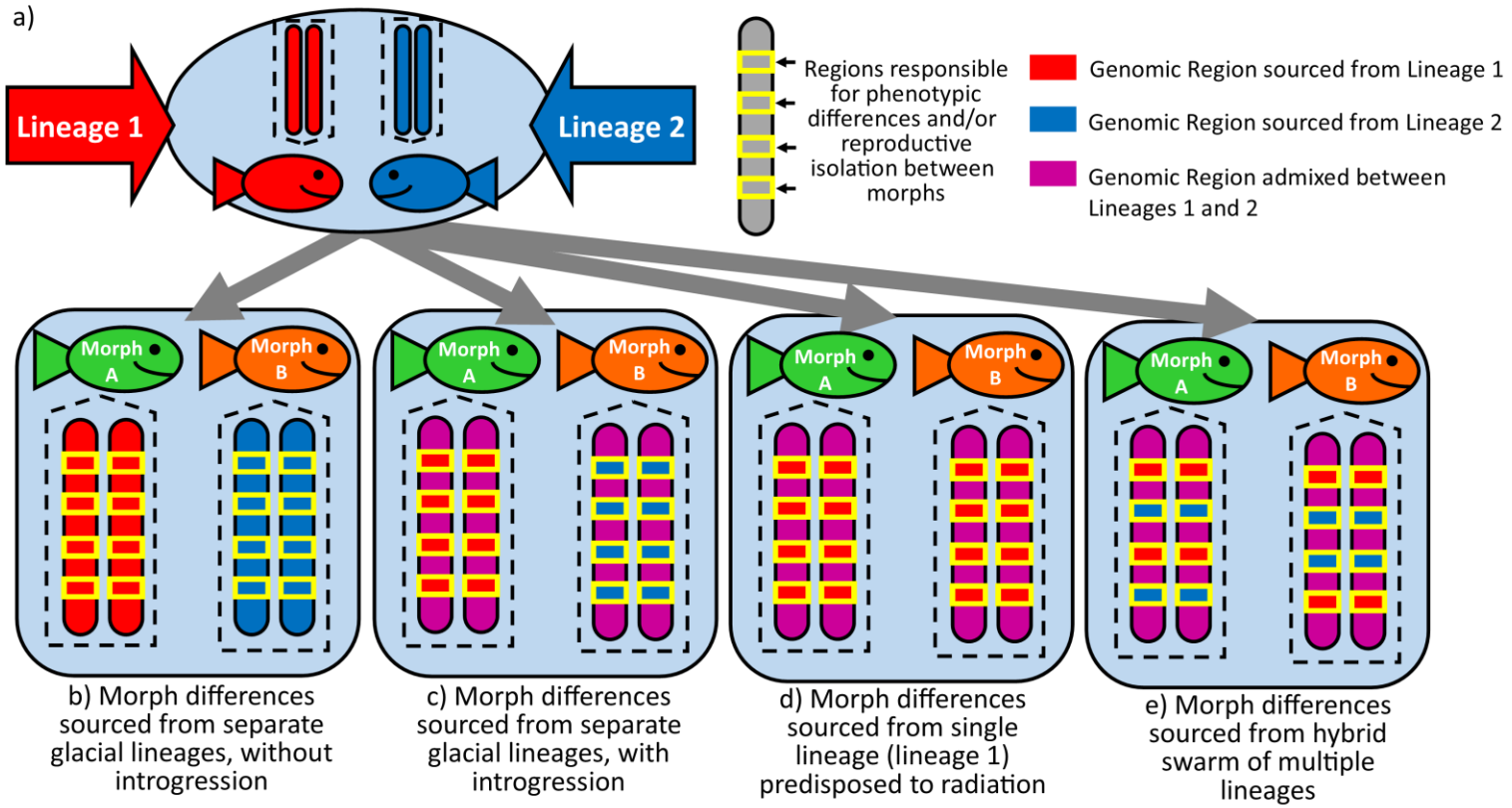

Fig.7.3 Potential modalities by which secondary contact of two glacial lineages (a) lineage 1 – red, lineage 2- blue) could influence the subsequent genetic differentiation of sympatric morphs (purple and orange) in descendant populations: b) glacial lineages may fail to introgress such that the genetic character of each sympatric morph is derived from a separate glacial lineage, c) glacial lineages introgress but only at genomic regions not contributing to the genetic differentiation of sympatric morphs such that the genetic character of each sympatric morph is still derived from a separate glacial lineage, d) glacial lineages introgress and the genomic regions contributing to the genetic differentiation of sympatric morphs are from a single lineage which is predisposed to radiation, e) glacial lineages introgress and novel combinations of alleles sourced from multiple lineages contribute to the genetic differentiation of sympatric morphs.

7.10 Tables

Table 7.1 Sympatric morphs demonstrating significant genetic differences by species and morph differentiation type within Salmonidae. Checkmarks indicate that significant genetic differences have been observed.

Species	Migratory Life History	Spawning Location	Spawning or Run Time	Trophic Level or Morphology	Cryptic
Coregonus albula			✓		
Coregonus artedi				✓	
Coregonus clupeaformis		✓	✓	✓	
Coregonus lavaretus		✓	✓	✓	
Oncorhynchus gorbuscha			✓		
Oncorhynchus mykiss	✓	✓	✓		
Oncorhynchus nerka	✓	✓	✓		
Oncorhynchus tshawytscha			✓		
Prosopium spp.				✓	
Salmo salar	✓	✓	✓		
Salmo trutta	✓	✓	✓	✓	✓
Salvelinus alpinus	✓	✓	✓	✓	✓
Salvelinus fontinalis	✓	✓		✓	
Salvelinus malma					✓
Salvelinus namaycush				✓	✓

Table 7.2 List of species and papers where nuclear genetic variation among sympatric and allopatric morphs was best explained by geography, not morph type.

Species	Citation
Coregonus spp.	Vuorinen et al. 1981; Bodaly et al. 1992; Campbell and Bernatchez 2004; Østbye et al. 2005b, 2006; Schulz et al.; 2006; Delling et al. 2014; Piette-Lauzière et al. 2019
O. mykiss	Docker and Heath 2003; Narum et al. 2004; McPhee et al. 2007; Olsen et al. 2006; Heath et al. 2008; Arciniega et al. 2016; Prince et al. 2017
O. nerka	Taylor et al. 1996; Beacham et al. 2006c; McPhee et al. 2009; Gomez-Uchida et al. 2011; Frazer and Russello 2013; Veale and Russello 2017b; Larson et al. 2019
O. tshawytscha	Utter et al. 1989; Teel et al. 2000; Waples et al. 2004; Beacham et al. 2006a; Brieuc et al. 2015; Prince et al. 2017
S. alpinus	Hindar et al. 1986; Gíslason et al. 1991; Volpe et al. 1996; Alekseyev et al. 2009; Kapralova et al. 2011; Gordeeva et al. 2015; Jacobs et al. 2020
S. fontinalis	Jones et al. 1997
S. namaycush	Harris et al. 2015; Bernatchez et al. 2016
S. salar	Adams et al. 2016

Table 7.3 Degree of parallelism of genetic differentiation among sympatric salmonid morphs in 11 studies. Outlier loci were those demonstrating significant differences among sympatric morphs. Loci were designated as demonstrating parallelism if they were detected as outliers among sympatric morphs in two or more locations of sympatric morphs. The proportion of outlier loci also demonstrating parallelism is given in brackets.

Study	Species	Morph Differentiation	Loci Type	Total loci	Outlier loci	Parallel outlier loci
Mehner et al. 2010	*C. albula*	spring vs. fall spawning	AFLPs	1244	95	3 (0.03)
Campbell and Bernatchez 2004	*C. clupeaformis*	dwarf vs. normal	AFLPs	440	48	6 (0.13)
Renaut et al. 2011	*C. clupeaformis*	dwarf vs. normal	SNPs	96	22	4 (0.18)
Feulner and Seehausen 2019	*Coregonus sp.*	large benthic vs. small benthic, large benthic vs. planktivore	SNPs	16173	65	4 (0.06)
Hudson et al. 2013	*C. lavaretus*	up to 5 morphologically or trophically differentiated morphs	AFLPs	835	96	10 (0.10)
Limborg et al. 2014	*O. gorbuscha*	odd vs. even year spawners	SNPs	8036	24	4 (0.17)
Frazer and Russello 2013	*O. nerka*	beach vs. stream spawning (Kokanee Salmon)	microsatellites	50	15	4 (0.27)
Nichols et al. 2016	*O. nerka*	Sockeye Salmon vs. Kokanee Salmon	SNPs	2593	172	2 (0.01)
Veale and Russello 2017b	*O. nerka*	Sockeye Salmon vs. Kokanee Salmon	SNPs	6568	334	68 (0.20)
Salisbury et al. 2020	*S. alpinus*	small vs. big	SNPs	14404-22603 (location dependent)	1195	38 (0.03)
Perreault-Payette et al. 2017	*S. namaycush*	lean vs. humper vs. siscowet vs. redfin	SNPs	6822	901	67 (0.07)

Table 7.4 Outlier genes differentiating sympatric salmonid morphs in multiple species. Putative functions were determined from UnitProtKB (UniProt Consortium 2007).

Gene	Putative Function	Gene Name	Study	Species	Morph
Ankycorbin	cell differentiation, spermatogenesis	Ankycorbin	Arostegui et al. 2019	*O. mykiss*	fluvial vs. adfluvial
		Ankycorbin isoform X1	Lemopoulos et al. 2018	*S. trutta*	resident vs. migratory
Cullin-9-like	Ubl conjugation pathway	Cullin-9-like	Nichols et al. 2016	*O. nerka*	resident vs. anadromous
		Cullin-9-like	Perreault-Payette et al. 2017	*S. namaycush*	lean vs. humper vs. siscowet vs. redfin
Desmoplakin	cell-cell adhesion	Desmoplakin	Argostegui et al. 2019	*O. mykiss*	fluvial vs. adfluvial
		Desmoplakin isoform x1	Perreault-Payette et al. 2017	*S. namaycush*	lean vs. humper vs. siscowet vs. redfin
FERM and PDZ domain-containing protein 3-like	cytoskeleton component	FERM and PDZ domain-containing protein 3-like isoform X4	Lemopoulos et al. 2018	*S. trutta*	resident vs. migratory
		FERM and PDZ domain-containing protein 3-like isoform x1	Perreault-Payette et al. 2017	*S. namaycush*	lean vs. humper vs. siscowet vs. redfin
Fidgetin	ATP binding	Fidgetin	Hale et al. 2013	*O. mykiss*	resident vs. anadromous
		Fidgetin-like	Perreault-Payette et al. 2017	*S. namaycush*	lean vs. humper vs. siscowet vs. redfin
Growth arrest-specific protein 1	cell cycle, growth arrest	Growth arrest-specific protein 1	Guðbrandsson et al. 2019	*S. alpinus*	small benthic vs. large benthic vs. planktivorous, vs. piscivorous
		Growth arrest-specific 1a precursor	Hale et al. 2013	*O. mykiss*	resident vs. anadromous
Heat-shock protein HSP 90	protein folding	Heat-shock protein HSP 90	Renaut et al. 2011	*C. clupeaformis*	dwarf vs. normal
		Heat shock protein HSP 90-alpha-like	Veale and Russello 2017b	*O. nerka*	resident vs. anadromous
Latent-transforming growth factor beta-binding protein 3	calcium ion binding	Latent-transforming growth factor beta-binding protein 3	Lemopoulos et al. 2018	*S. trutta*	resident vs. migratory
		Latent-transforming growth factor beta-binding protein 3 isoform x1	Perreault-Payette et al. 2017	*S. namaycush*	lean vs. humper vs. siscowet vs. redfin

Table 7.4 Continued.

Gene	Putative Function	Gene Name	Study	Species	Morph
Malate dehydrogenase	carbohydrate metabolism	Malate dehydrogenase	Frazer and Russelo 2013	*O. nerka*	beach-spawning vs. stream-spawning
		Malate dehydrogenase	Hale et al. 2013	*O. mykiss*	resident vs. anadromous
MHC class I	immune response	MHC class I a region	Feulner and Seehausen 2019	*C. lavaretus*	large benthic vs. small benthic vs. planktivore
		MHC class I a region	Hale et al. 2013	*O. mykiss*	resident vs. anadromous
MHC Class II	immune response	MHC Class II	Conejeros et al. 2014	*S. alpinus*	small vs. large, pale vs. dark
		MHC Class II	Gomez-Uchida et al. 2011	*O. nerka*	island beach spawner vs. mainland beach spawner vs. stream spawner
		MHC Class II	Larson et al. 2014	*O. nerka*	beach spawner vs. river spawner vs. stream spawner Sockeye Salmon
		MHC Class II	Lehnert et al. 2016	*O. nerka*	red vs. white
		MHC Class II	McGlauflin et al. 2011	*O. nerka*	beach spawner vs. river spawner vs. stream spawner
Mitochondrial intermediate peptidase-like	metal binding	Mitochondrial intermediate peptidase-like	Elias et al. 2018	*S. fontinalis*	fluvial vs. adfluvial, coasters vs. resident
		Mitochondrial intermediate peptidase-like	Nichols et al. 2016	*O. nerka*	resident vs. anadromous
Nuclear pore complex protein Nup88-like	ribosomal subunit export from nucleus	Nuclear pore complex protein Nup88-like isoform X2	Lemopoulos et al. 2018	*S. trutta*	resident vs. migratory
		Nuclear pore complex protein Nup88-like	Nichols et al. 2016	*O. nerka*	resident vs. anadromous
Plexin-A2-like	semaphoring receptor activity	Plexin-A2-like	Lemopoulos et al. 2018	*S. trutta*	resident vs. migratory
		Plexin-A2-like	Nichols et al. 2016	*O. nerka*	resident vs. anadromous
Probable phosphatase phospho1	metal ion binding	Probable phosphatase phospho1 isoform X2	Lemopoulos et al. 2018	*S. trutta*	resident vs. migratory
		Probable phosphatase phospho1	Nichols et al. 2016	*O. nerka*	resident vs. anadromous

Table 7.4 Continued.

Gene	Putative Function	Gene Name	Study	Species	Morph
Protein NLRC3-like	inflammatory response, immune response, regulation of apoposis	Protein NLRC3-like	Lemopoulos et al. 2018	*S. trutta*	resident vs. migratory
		Protein NLRC3-like	Perreault-Payette et al. 2017	*S. namaycush*	lean vs. humper vs. siscowet vs. redfin
Protocadherin-18	cell adhesion, nervous system development	Protocadherin-18	Hale et al. 2013	*O. mykiss*	resident vs. anadromous
		Protocadherin-18 isoform X1	Lemopoulos et al. 2018	*S. trutta*	resident vs. migratory
Ribulose phosphate 3 epimerase	carbohydrate metabolism	Ribulose-phosphate 3-epimerase-like	Lemopoulos et al. 2018	*S. trutta*	resident vs. migratory
		Ribulose phosphate 3 epimerase	Renaut et al. 2011	*C. clupeaformis*	dwarf vs. normal
Spondin-1-like	transmembrane protein	Spondin-1-like	Lemopoulos et al. 2018	*S. trutta*	resident vs. migratory
		Spondin-1-like	Perreault-Payette et al. 2017	*S. namaycush*	lean vs. humper vs. siscowet vs. redfin
Thrombospondin-1	cell adhesion, inflammatory response, negative regulation of angiogenesis	Thrombospondin-1a	Hale et al. 2013	*O. mykiss*	resident vs. anadromous
		Thrombospondin-1-like	Lemopoulos et al. 2018	*S. trutta*	resident vs. migratory
Transmembrane protein 121-like	transmembrane protein	Transmembrane protein 121-like	Lemopoulos et al. 2018	*S. trutta*	resident vs. migratory
		Transmembrane protein 121-like	Veale and Russello 2017b	*O. nerka*	Black resident Kokanee Salmon vs. anadromous Sockeye Salmon
Unconventional myosin-XVIIIa-like	actin filament binding, ATP binding, motor activity	Unconventional myosin-XVIIIa-like	Elias et al. 2018	*S. fontinalis*	fluvial vs. adfluvial, coasters vs. resident
		Unconventionalonal myosin-XVIIIa-like isoform x3	Perreault-Payette et al. 2017	*S. namaycush*	lean vs. humper vs. siscowet vs. redfin

Table 7.4 Continued.

Gene	Putative Function	Gene Name	Study	Species	Morph
VPS10 domain-containing receptor SorCS1-like	transmembrane protein	VPS10 domain-containing receptor SorCS1-like	Elias et al. 2018	*S. fontinalis*	fluvial vs. adfluvial, coasters vs. resident
		VPS10 domain-containing receptor SorCS1-like	Veale and Russello 2017b	*O. nerka*	Black resident Kokanee Salmon vs. anadromous Sockeye Salmon
Zinc finger e-box-binding homeobox 2-like	DNA-binding	Zinc finger e-box-binding homeobox 2-like	Perreault-Payette et al. 2017	*S. namaycush*	lean vs. humper vs. siscowet vs. redfin
		Zinc finger e-box-binding homeobox 2-like	Veale and Russello 2017b	*O. nerka*	shore-spawning vs. stream-spawning (resident Kokanee Salmon)

7.11 Appendices

7.11.1 Appendix I

Populations of several salmonid species demonstrate closer genetic affinity among allopatric morphs than sympatric morphs. For example, allopatric coregonid morphs in some neighbouring Swiss lakes were more genetically similar than sympatric morphs, potentially as a result of morphs arising originally in the large paleolakes which encompassed contemporarily neighbouring lakes (Hudson et al. 2011). While upstream of the mid-Fraser Kokanee Salmon were more closely related to sympatric Sockeye Salmon, Kokanee Salmon in the Columbia River, south Thompson River, and the mid-Fraser River were found to form a monophyletic clade (Beacham and Withler 2017). This is potentially a result of ongoing gene flow among Kokanee Salmon populations in this region which have eroded genetic signatures of their polyphyletic origin (Johannesson 2001). Alternatively, Kokanee Salmon may have a true monophyletic origin in this region, arising in a single locality before colonizing the region. Arctic Charr morphs from Iceland, the British Isles and Scandinavia were generally most genetically similar to their sympatric morph; however, sympatric morphs in Loch Tay, Loch Stack, Loch Maree and Fjellfrosvatn were not monophyletic to each other (Wilson et al. 2004). Significant nuclear and mitochondrial genetic differences suggest ferox Brown Trout colonized Lough Melvin prior to the Brown Trout ancestor from which the gillaroo and sonaghen morphs descended (Ferguson and Mason 1981; Ferguson and Taggart 1991; McVeigh et al. 1995). The significant genetic differences found among Brook Trout spawning in the inflows and outflows of Lake Mistassini suggest they were founded by independent colonization events from one or both of the Atlantic and Mississipian refugia (Fraser and Bernatchez 2005).

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CHAPTER 8 - DISCUSSION

8.1 Summary

My thesis work reveals Labrador to be an important "hotspot" of Arctic Charr morph diversity. Similar charr diversifications have been well-studied in landlocked populations in Transbaikalia, Iceland, Scandinavia, and Scotland (Markevich and Esin 2018). However, this thesis work demonstrates Labrador to be relatively unique to these hotspots as it contains not only sympatric landlocked morphs but also resident and anadromous morphs (but see Nordeng 1983; Kapralova et al. 2011 for evidence of all three morph types in Scandinavia and Iceland, respectively). Furthermore, because charr populations were recently established in Labrador after this regions' deglaciation ~9000 years BP (Bryson et al. 1969; Occhietti et al. 2011), genetic comparisons among morphs in this thesis has allowed for the detection of early genetic signatures of incipient speciation and adaptation. My investigation of the historical colonization of Labrador has shown that contemporary populations were likely established by a common anadromous ancestral population resulting from the introgression of the Arctic, Atlantic, and Acadian lineages (though the extent of introgression likely differs across Labrador). This recent common ancestry has facilitated an assessment of the degree of genomic parallelism contributing to morph differentiation (while minimizing the potential for non-parallelism due to differing evolutionary histories). This thesis has therefore contributed to our understanding of 1) the genetic relationships among morphs, 2) the influence of colonization history on morph evolution, 3) the predictability of morph evolution.

8.1.1 Genetic Relationships Among Morphs

A key outcome of my thesis work is the identification of genetically distinguishable anadromous, resident, and landlocked morphs within a relatively small geographic region in Labrador. In Chapter 2 I characterized the neutral genetic relationships among landlocked and anadromous populations of Arctic Charr in three drainages within Labrador, Canada. Here, I identified a single location (Ramah) with genetically distinguishable, size-differentiated morphs, suggestive of resident and anadromous morphs, respectively. To my knowledge this represents the first such

observation of sympatric resident and anadromous morphs that are genetically distinguishable at neutral markers. Excitingly, this has been subsequently observed in charr in Greenland (Doenz et al. 2019) and Svalbard (O'Malley et al. 2019). Chapter 4 confirmed the genetic distinctiveness between these sympatric morphs using SNPs, and Chapters 5 and 6 indicate that the "big" morph within Ramah is genetically consistent with other anadromous populations. In Chapter 2 I also found evidence of genetically distinguishable sympatric morphs occurring in each of two landlocked lakes (WP132, WP133). Subsequent analysis of these lakes in Chapter 5 using SNPs confirmed their genetic distinctiveness and revealed these morphs to be size-differentiated. Similar size-differentiated morphs were also discovered in Lonely Lake, Brooklyn Lake, and Esker North Lake (Chapter 4, 5). While the big morph detected in the latter two lakes were initially suggested to be anadromous in Chapter 4 due to the fact that these lakes were considered sea-accessible by Anderson (1985), subsequent analyses in Chapter 5 and 6 indicated that these big morphs are more genetically distinguishable from anadromous populations than expected. This is potentially due to low or no gene flow with other anadromous populations, suggesting that these morphs may no longer be anadromous. Chapters 2, 5, 6 demonstrated the genetic distinctiveness of landlocked and resident populations in comparison to anadromous populations. Landlocked populations also demonstrated reduced nuclear and mitochondrial diversity relative to anadromous populations (Chapter 3, 6). Resident and landlocked populations were generally found at higher altitudes which may have directly prevented migration in these populations (Chapter 6). Alternatively, straying has likely contributed to anadromous populations' elevated genetic diversity and reduced genetic differentiation (Chapter 6). In addition to neutral processes, morph genetic structure was also characterized by adaptation and I found evidence for selection between sympatric size-differentiated morphs (Chapters 4, 5) and allopatric landlocked and anadromous morphs (Chapter 5). At a larger spatial scale, all populations (regardless of morph) showed a clear pattern of isolation by distance (IBD) (Chapter 6). This pattern is likely driven by both geographic distance as well as selection due to environmental clines in temperature and precipitation (Chapter 6). The genetic relationships among Arctic Charr morphs within Labrador are therefore influenced by the interactive effects of both neutral and adaptive processes.

8.1.2 Colonization History and Morph Evolution

Beyond contemporary processes, historical colonization has played an important role in charr evolution in this region. In Chapter 3 I used mtDNA D-loop haplotypes to uncover evidence of extensive secondary contact and introgression of the Arctic lineage, Atlantic lineage, and to a lesser extent Acadian lineage across Labrador charr populations. However, the haplotypes associated with all three of these lineages were found in both landlocked and anadromous populations. In addition, there was no difference in the character of mtDNA haplotypes between sympatric morphs in any of the locations in Labrador and Newfoundland where sympatric morphs were detected (Chapter 2, 3, 4, 5), suggesting that morphs were not founded by distinct glacial lineages. However, the significant correlation between latitude and genetic diversity in anadromous Labrador populations (Chapter 6) may reflect greater historical introgression of nuclear genetic material between the Atlantic and Arctic lineages in northern Labrador. This introgression event may also partially explain the greater genetic diversity in northern Labrador charr populations in comparison to those in southern Labrador, Newfoundland, and Ungava. Given that secondary contact has been hypothesized to fuel radiation events in European whitefish (Hudson et al. 2007, 2011) and cichlids (Meier et al. 2017), the importance of the colonization history to contemporary morph differentiation within Labrador is an intriguing area for future research.

8.1.3 The Predictability of Morph Evolution

The presence of replicate morph populations within Labrador has provided a natural experiment to test the repeatability of genetic differentiation both between sympatric small and big morphs in landlocked or sea-accessible populations (Chapter 4, 5) and between allopatric landlocked and anadromous populations (Chapter 5). Generally, there was little evidence of genetic parallelism, as the majority of outlier loci were only detected in a single paired comparison of allopatric or sympatric morphs. In addition, no single SNP, gene, or paralog consistently differentiated sympatric or allopatric populations. However, there was evidence of several SNPs, genes, and paralogs demonstrating parallelism in the majority of pairs considered. A single gene, pappalysin-2, which is associated with growth in humans and mice (Conover et al. 2011; Dauber et

al. 2016), consistently differed between size-differentiated sympatric morphs in Ramah, Brooklyn, and Esker North Lakes (Chapter 4) but not in two other locations (Chapter 5). Another gene, myomesin-2, which is associated with fast-twitch muscle function (Schoenauer et al. 2008), also consistently differentiated allopatric landlocked and anadromous populations in five of seven pairs. A region on chromosome AC17 intriguingly differentiated putative resident and anadromous sympatric morphs in Ramah (Chapter 4), as well as landlocked and anadromous populations elsewhere (Chapter 5). This genomic region on chromosome AC17, along with the genomic region on chromosome AC21 containing myomesin-2 was also detected as an environmentally associated outlier regions in populations across Labrador (Chapter 6). These results suggest the re-use of certain genetic pathways for morph differentiation and support the existence of genetic parallelism. Further investigation of the developmental consequences and evolutionary history of these candidate genes and genomic regions are required to confirm and contextualize their importance to morph differentiation.

8.2 Thesis Applications for Conservation and Industry

My thesis work has several implications for both conservation and aquaculture practices. The extensive introgression apparent between the Atlantic, Arctic, and Acadian lineages within Newfoundland and Labrador suggests no need to manage glacial lineages independently. However, populations outside of this secondary contact zone may have lower genetic diversity and therefore be more vulnerable to environmental change (Chapter 6). Landlocked populations generally demonstrated lower genetic diversity than anadromous populations. However, this diversity was largely stable over the last 20 generations (Chapter 6), suggesting that despite their genetic isolation, landlocked populations are not necessarily more vulnerable to extinction than anadromous populations. This is consistent with the stronger selection anticipated against anadromy with increasing temperatures and primary productivity due to climate change (Reist et al. 2006; Finstad and Hein 2012). Given their genetic distinctiveness, landlocked and resident populations should be managed separately from anadromous populations. However, gene flow is possible from landlocked to anadromous populations (as was observed in Chapters 2, 3) and between sympatric resident and anadromous morphs. In

accordance with the "transporter hypothesis" (Schluter and Conte 2009), this may have important evolutionary implications for facilitating the founding of future non-anadromous populations by anadromous population (see section 7.3.3 below). However, the importance of gene flow from non-anadromous to anadromous populations on a contemporary time frame may be minimal (but future research comparing anadromous populations with and without gene flow from a nearby landlocked population could clarify this).

The candidate SNPs, genes, paralogs, and genomic regions I have identified as potentially important for sympatric differentiation of big and small morphs, as well as between landlocked and anadromous populations have important implications for informing morph management. These candidate loci may be useful for the detection of anadromous populations which are trending towards a non-anadromous genetic profile. Furthermore, the candidate loci differentiating small and big morphs identified in Chapters 4 and 5 may be useful to select against small body size which is an undesirable trait in the Arctic Charr aquaculture industry (Yossa et al. 2019). The characterization of the neutral and adaptive differentiation between Arctic Charr morphs in this thesis therefore provides important knowledge for informing future conservation and aquaculture practices.

8.3 Future Research

My work leaves several questions about morph differentiation in charr unanswered while also prompting new ones. Below, I elaborate on five burning questions inspired from this thesis work, in some cases providing speculative hypotheses and potential ways to test them.

8.3.1 What is the relationship between small and big morphs in landlocked and sea-accessible populations?

One surprising result of this thesis work was that the sizes of the sympatric putative resident and anadromous morphs (e.g., in Ramah) were similar to those observed in sympatric small and big landlocked morphs (e.g., in WP132, WP133). Small morphs typically had a mean/median length ~ 200 mm while big morphs had a mean/median

length >> 200 mm. I speculate that the small and big morphs in landlocked populations may have been ancestrally resident and anadromous morphs, respectively. In this scenario the big morph would have lost its capacity for anadromy more recently than the small morph perhaps due to a physical barrier (such as a waterfall) or by selection due to increasing migratory costs. In support of this hypothesis is the observation that large non-anadromous morphs of charr are less derived and more morphologically similar to anadromous morphs than they are to small non-anadromous morphs (Nordeng 1983; Kapralova et al. 2011). In addition, this transition from sympatric anadromous and resident morphs to landlocked big and small morphs may have been observed in Svalbard. Here, large resident morphs were genetically indistinguishable from sympatric anadromous morphs but both were genetically distinguishable from sympatric small resident morphs (O'Malley et al. 2019). This suggests that anadromous morphs may become large residents due to plasticity and that the reproductive isolation between large and small non-anadromous morphs may have arisen prior to the total loss of anadromy of the large morph. Alternatively, small and big morphs may have evolved from a homogeneous non-anadromous population (though potentially using some of the same genetic pathways used to differentiate sympatric anadromous and resident morphs). It is also possible that the timing of morph differentiation with respect to the loss of anadromy may differ between locations. Given that drift may quickly erode signatures of anadromy in landlocked morphs, knowing whether sympatric morphs diverged before or after the loss of anadromy may be difficult without "catching" morph differentiation in real-time. Recently landlocked and monomorphic charr populations could therefore be monitored for morph differentiation. Alternatively, genetic characterization of very recently evolved, non-anadromous sympatric small and big morphs could be helpful to test whether these morphs arose before or after the loss of anadromy.

8.3.2 How important are paralogs to morph differentiation?

The whole genome duplication in salmonids ~ 88 mya (Macqueen and Johnston 2014) has resulted in an abundance of paralogs in salmonids, some of which are still tetrasomically inherited (Mckinney et al. 2016). It is therefore possible that these paralogs have facilitated morph differentiation (Macqueen and Johnston 2014), particularly

through neofunctionalization (Robertson et al. 2017). Alternatively, if paralogs retain similar functionality as has been suggested by QTL analysis in other salmonids (Nichols et al. 2008; Norman et al. 2011), then different paralogous copies of the same gene may contribute to similar morph differentiation. My results found evidence for different paralogous copies of the same gene consistently differentiating sympatric, size-differentiated morphs (Chapter 4) and allopatric landlocked and anadromous morphs (Chapter 5). Such genetic parallelism at the level of the paralog may therefore play an important but underappreciated role in morph differentiation (Otto and Whitton 2000; Nichols et al. 2008; Conte et al. 2012; Chen et al. 2019) as paralogs are often discarded prior to analyses (Limborg et al. 2016; Mckinney et al. 2016). Sequencing the paralogs demonstrating parallelism in this thesis could be informative of their function and importance to morph differentiation in Arctic Charr. Additionally, further investigation of the importance of paralogs to morph formation is needed in other polymorphic species (and particularly other salmonids).

8.3.3 Are Arctic Charr subject to the transporter hypothesis?

Landlocked and resident forms of Arctic Charr might be considered evolutionary "dead ends" because of their genetic isolation. However, my thesis work reveals that some gene flow may be possible between these non-anadromous morphs. Arctic Charr might therefore conform to the "transporter hypothesis" where a migratory morph facilitates the movement of adaptive alleles between locally adapted non-migratory morphs (Schluter and Conte 2009). Gene flow is likely not possible from anadromous charr to landlocked charr populations (Chapter 5, 6). However, downstream gene flow from landlocked populations and from sympatric resident populations could provide anadromous populations with the adaptive genetic variation necessary to found future non-anadromous populations as predicted by the transporter hypothesis (Schluter and Conte 2009). In addition to adaptive variation, non-anadromous morphs of Arctic Charr might seed anadromous populations with genetic variation that has deleterious epistatic effects with existing standing variation in the anadromous populations (i.e., Bateson-Dobzhansky-Muller incompatibilities (Bateson 1909; Muller 1942; Dobzhansky 1982; Cutter 2012; Marques et al. 2019)). Such incompatibilities are expected to arise in non-

anadromous populations due to their inherent genetic isolation. However, if such incompatibilities are not selected out of the anadromous morph then they could be selected for in future colonizing populations to prompt reproductive isolation (i.e., between landlocked morphs or between resident and anadromous morphs). Given that the anadromous form is most likely to survive through glacial periods (Power 2002a), gene flow from non-anadromous to anadromous populations could therefore facilitate the diversification of Arctic Charr through glacial cycles. This phenomenon may also contribute to the observed genetic parallelism between sympatric morphs (Chapter 4, 5) and between allopatric landlocked and anadromous morphs (Chapter 5). Similar to *Eda* in marine Three-Spined Sticklebacks (*Gasterosteus aculeatus*) (Colosimo et al. 2005; Schluter and Conte 2009; Nelson and Cresko 2018), old standing genetic variation in the colonizing anadromous Arctic Charr morph could be selected upon to drive repeated morph radiation. Sequencing the genes and genomic regions which demonstrate parallelism in this thesis would be useful to determine if the alleles at these loci are anciently derived as predicted by the transporter hypothesis. Furthermore, a comparison of Arctic Charr morphs across a greater spatial scale, as has been done in sticklebacks (Magalhaes et al. 2020), would be useful to test if the loci demonstrating parallelism in Labrador do so across the Arctic Charr range.

8.3.4 Why do sympatric morphs evolve in some locations but not others?

The presence of sympatric genetically distinguishable morphs in a minority of those locations sampled in Labrador begs the question as to what drives morph differentiation in these locations but not others. Environments occupied by monomorphic populations may lack the multiple available niches responsible for the divergent selection necessary for the evolution and continued persistence of sympatric morphs (Robinson and Wilson 1994; Smith and Skúlason 1996). Indeed, multiple charr morphs are more commonly found in larger, deeper, and more spatially complex lakes with few other fish species (Griffiths 1994; Riget et al. 2000). Greater genetic divergence between sympatric morphs is also observed between more morphologically and ecologically differentiated morphs (Gíslason et al. 1999; Corrigan et al. 2011; Conejeros et al. 2014; Gordeeva et al. 2015). Though my work revealed sympatric morphs in larger lakes such as Esker North

and Brooklyn, I also detected sympatric in much smaller lakes such as Ramah, and the WP lakes (WP132, WP133). The ability for sympatric morphs to spawn at different times may also play a role in the evolution of sympatric morphs. Longer and more stable marine periods might allow for discrete spawning times for sympatric resident and anadromous morphs, leading to isolation by time (Hendry and Day 2005). In support of this hypothesis is the observation that mature female resident charr from Ramah Lake had eggs at a later stage of development than those of sympatric mature female anadromous charr (Ruzzante and Perry pers obs). Spawning time differences have also been observed among morphs in other populations (Westgaard et al. 2004; Corrigan et al. 2011; Garduno-Paz et al. 2012). However, longer marine periods are not likely to necessitate morph differentiation of a resident morph since anadromous populations in close proximity to Ramah (with presumably similar marine periods) did not demonstrate a genetically distinguishable sympatric resident morph. Additionally, a short marine period also did not prevent the evolution of sympatric, genetically distinguishable resident and anadromous morphs in Linne`vatn, Svalbard (O'Malley et al. 2019). Nearby anadromous morphs in Lake Dieset (~150 km north of Linne`vatn) have an average marine period of only 33.6 days (Gulseth and Nilssen 2000) though this can vary significantly annually (Svenning and Gullestad 2002). In comparison, anadromous fish from the Fraser River, Labrador (~250 km south of Rammah) have a marine period of ~ 3 months from May to August (Dempson and Green 1985). Therefore, future investigation of the ecological differences between the sympatric morphs in Labrador identified by this thesis work as well as the physical and environmental characteristics of the lakes they occupy is needed to reveal the selective pressures driving morph differentiation both between landlocked sympatric morphs and between sympatric resident and anadromous morphs.

In addition to an absence of divergent selection, a lack of genetic variation to respond to divergent selection might have also hampered morph formation in some lakes. If landlocked populations experienced bottlenecks due to founder effects, the population may not have retained sufficient standing genetic variation to undergo morph differentiation. The presence of sympatric morphs in the genetically depauperate WP lakes (WP132, WP133) somewhat belies this argument, though this loss of genetic diversity could have occurred subsequent to morph differentiation.

The availability of standing variation may be more important to facilitating sympatric morph differentiation across the species range. Neutral genetic differences have been observed between sympatric morphs in Labrador (Chapters 1-5), Quebec (Power et al. 2009), Alaska (May-Mcnally et al. 2015b), Greenland (Doenz et al. 2019), Svalbard (O'Malley et al. 2019), Scandinavia (Østbye et al. 2020), but not between morphologically distinct sympatric morphs in the Canadian High Arctic including populations on Baffin Island (Moore et al. 2014), and Ellesmere Island (Arbour et al. 2011). The high Canadian Arctic was likely founded by only the Arctic lineage, which is older and less genetically diverse than the other lineages (Moore et al. 2015). Populations founded by this lineage may therefore not have had the genetic variation necessary to evolve genetically distinguishable sympatric morphs. However, the absence of genetic differentiation among morphs in the Canadian high Arctic could also be due to a greater capacity for plasticity, lower divergent selection, or a more recent origin of morphs such that not enough time has elapsed for neutral genetic differences to accumulate. Interestingly, I only observed a maximum of two genetically distinguishable sympatric morphs in Labrador locations, though three to five sympatric morphs have been described in Scandinavia (Østbye et al. 2020), Iceland (Guðbrandsson et al. 2019), and Greenland (Doenz et al. 2019). Again, it is unclear as to whether the number of morphs in Labrador is limited due to a lack of selection or due to a lack of genetic variation (though the latter seems unlikely given the historical introgression of three glacial lineages in Labrador). An investigation of Arctic Charr populations with and without sympatric morphs across its Holarctic distribution is needed to determine the relative importance of selection and genetic variation to morph differentiation.

8.3.5 What mechanisms drive genetic parallelism?

A general lack of genetic parallelism was detected between size-differentiated sympatric morphs and between allopatric landlocked and anadromous populations. Furthermore, no single locus consistently differentiated all sympatric or allopatric morph pairs. This suggests that morph differentiation can be accomplished by employing multiple alternative genetic pathways. This lack of genetic parallelism could be due to the availability of multiple genetic pathways to facilitate morph differentiation. The ancestral

whole genome duplication (WGD) in salmonids is one potential source of such genetic variation (Macqueen and Johnston 2014). Neofunctionalization subsequent to this WGD could have generated many genetic pathways to achieve similar morph differentiation (Robertson et al. 2017). Functionally similar homeologs might also be alternatively used in different locations to drive morph differentiation. The latter scenario, which would result in parallelism at the level of the paralog, was evident but did not consistently explain morph differentiation in all allopatric and sympatric morph pairs. Another potential source of genetic variation in Labrador populations is the ancestral introgression between multiple glacial lineages in this region (Chapter 3). We might therefore observe more evidence of genetic parallelism among replicate morphs of charr in regions colonized by a single lineage. Differing local selective pressures, or genetic drift could also prevent genetic parallelism (Campbell and Bernatchez 2004). In addition, it is possible that the ~ 20000 SNPs used in Chapters 4 and 5 missed parallel regions of the genome. Therefore, further investigation is needed to uncover what is driving the general lack of genetic parallelism (i.e., at the level of SNPs, genes, paralogs) among replicate charr morphs in Labrador.

However, a handful of SNPs, genes, paralogs, and genomic regions demonstrated evidence of parallelism in the majority of sympatric or allopatric paired morphs. The question then is why do these particular loci demonstrate parallelism? As mentioned above (see section 7.3.3), perhaps these loci represent old standing variation which has been repeatedly selected for to drive morph differentiation in charr. If loci demonstrating parallelism are the result of consistent selection, then comparisons of the developmental consequences between parallel and non-parallel loci contributing to morph differentiation could help us understand which phenotypic aspects of morph differentiation are predictable at the genetic level. Furthermore, comparison of the genetic architecture and historical contexts of parallel and non-parallel loci contributing to morph differentiation might help explain this predictability.

8.4 Conclusion

By characterizing the genetic relationships among landlocked, anadromous, and resident Arctic Charr morphs across Labrador, my thesis work has made a significant

contribution to both our knowledge of this species and to our fundamental understanding of the evolution of phenotypic variation. This thesis reveals Labrador to be a unique region within the Holarctic distribution of Arctic Charr where genetically distinguishable morphs can occur in sympatry or allopatry and where secondary contact had historically occurred between multiple glacial lineages. These properties make Labrador an ideal natural laboratory to investigate the influence of historical and contemporary processes on evolution. Labrador Arctic Charr are therefore likely to continue to be an ideal model for future inquiry into morph differentiation and incipient speciation.

8.5 References

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Name: Robert Perry Title: Species Manager, Yukon

Signature: Date: 2021/02/5

February 4, 2021

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Signature: Date: February 4, 2021

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Name: Daniel Ruzzante Title: Professor and Sarah's PhD supervisor

Signature: _ Date: Feb 4, 2021